

Some aspects of mathematical ecology¹

Leigh Van Valen
 Department of Biology
 University of Chicago
 Chicago, Ill. 60637
 Received April 4, 1975

ABSTRACT: Ordinary application of mathematical ecology can give nonsense as well as insight. Two recent examples illustrate some general points; other general considerations show the value of a diversity of approaches to ecological theory. Prediction and optimization can also be misleading. Verbal and other kinds of theory do different things; the judgment of one by the standards of another leads to caricature.

*

*

*

Introduction

Two recent papers in the *American Naturalist* exemplify unusually clearly some of the difficulties with mathematical ecology. Some general comments on such problems follow my specific critique. I discuss reasons why one can, although using ordinary premises validly in the usual way, produce nonsense as well as enlightenment; the examples are merely convenient recent ones.

Examples

Gill (1974) uses standard interpretations of the Lotka-Volterra equations to reach the astonishing conclusion that resource (exploitative) competition can never lead, by itself, to competitive exclusion. When one confronts this conclusion with the biology, however, it collapses. Given two or more species with the same ultimately regulating resource, which thereby fixes K , one species may simply be better at finding the resource than the other species. Or it may survive longer when the resource is in short supply. Or it may need less of the resource per individual and so the same environment may appear to it more coarse-grained.

One doesn't need equations to show that each case will, under broadly realized assumptions, lead to competitive exclusion. All one needs to do is follow the biology of reproduction and note the absence of a counterbalancing force until the extinction of all but one species. MacArthur's graphical procedure (1958, 1972; Vandermeer, 1973) translates these words to geometry and may be clearer to some people, but it has no more information than the words (relative to the present conclusion) and needs the same assumptions.

Namkoong and Roberds (1974) use age-class data for a plot of redwoods, the data being copied from a paper by Bosch (1971). Bosch in turn derived his data from a paper by Roy (1966). And Roy's data come from a paper by Fritz (1929).

In this sequence some interesting things happen. Most strikingly, the first two of the seven age classes in the 1974 table are absent from that of 1929, where the interval spanning these classes has the notation, "0-200 years--unknown". So what happened? As well as lumping Fritz's 100-year intervals for older trees into 200-year intervals, Roy gave 696 as the number of trees younger than 200 years. This is derived from Fritz's statements that there were 1263 trees that

*

*

*

¹This paper was rejected by the *American Naturalist*, the main reason given being its (then) lack of headings.

were over 12 inches in diameter at breast height (DBH) and 567 trees that both were over 18 inches DBH (sic) and had their ages determined as over 200 years. An unknown number of trees cut down were measured (and so included in the 1263) but were unsuitable for age determination because of rotted centers and the like; there is also no correction for the probable age bias in such factors. Moreover, in addition to these two biases and the discrepancy between 12 and 18 inches DBH, diameter is a poor criterion of age for redwoods (Roy, 1966) and there is no evidence given that 12 inches DBH even approximates the average diameter of 200-year-old trees in a mature stand.

Bosch (1971) restricted Roy's class of 0-200 years to 20-200 years (but kept the number 696 for it) and added a class of younger trees with 1000 members. This last class may be derived from Roy's statement, "Not counting more than 1000 trees under 12 inches in diameter. . . ." Application of this sentence would equate 12 inches DBH with 20 years rather than 200, still without evidence. Fritz had said of trees under 12 inches DBH that "there are certainly much more than a thousand". Bosch's new class alternatively may be derived from Roy's statement that, in general, "the average well stocked acre supports nearly 1000 stems at 20 years". But the plot censused for Fritz's paper was of 30 acres, not 1, and moreover Roy's statement comes from a study by Bruce (1923). Bruce's figure refers to the new growth that appears after logging, not to equilibrium replacement, and excludes all stems less than 2.6 inches DBH. Such carelessness with data seems common and is compatible with the view that facts are a necessary evil, useful only as specific examples of pre-existing theory. (A "test" of an obvious truth is mostly a test of the accuracy of the data.)

Ecological assumptions

I find it less interesting to see exactly what went wrong with Gill's argument, because I don't believe that mathematical ecology can make any such proofs. In population genetics, a closely allied subject, there are underlying regularities in transmission, origin, and recombination of genes. These regularities are well understood. Departures from them are easily handled, but the necessary addition of a complex superstructure creates some problems of applicability. Nevertheless much of the theory is widely true and it has illuminated part of the mechanism of evolution. But the theory must merge with ecology, developmental biology, and other subjects to be really explanatory. Now, for the most part (despite various probings) it bumps into ecology and even the phenotype in general and stops.

The fundamental processes in ecology are the growth and regulation of populations. We can't treat the evolution of individuals as we can that of genes; populations give the lowest workable unit. It is possible to calculate an analog of the population growth rate r_m (or in general the r_t of Van Valen, 1973a) for individuals, and I have in ^m fact done this ^t experimentally (Van Valen, 1968 and unpublished). However, a detailed theory at this level rapidly becomes inordinately complex. And unfortunately populations grow in different ways. There is no theory that is detailed, general, and true, unlike the case on the comparable level in population genetics.

The problem is that when we use the good approximate theory based on logistic growth to draw conclusions, we don't know to what extent the conclusion depends on the true aspects or on the approximations. To the extent that we do know this, we have supported our conclusions by information outside the theory. Sometimes such information is all that is necessary, and the formal theory itself is superfluous. In other cases the additional information, which may take the form of another theory, is itself approximate but in a different way. We can then

hope that, as Levins (1966) put it, truth is the intersection of independent lies. But more frequently the theory itself is the only basis for conclusions, and all such conclusions must be sharply suspect. (Gill's conclusion needs, among other things, the common assumption that resource competition is at least as severe within species as among species. This is often false, as for competition for grass by sheep and cattle.) When mathematical assumptions rather than biological ones seem too restrictive, biologists should consider creating their own mathematics (cf. Blum, 1973; Jolicoeur and Heusner, 1971; Van Valen, 1964, 1974b; Wright, 1921).

Many theories are true when their assumptions are not, but if any general statement about a class of such cases can be made, it can be transformed into a more realistic assumption in the theories themselves. An original assumption may be generalized, or the theory may need to be derived in different ways for different cases. In theories as in faces, beauty can be an artifact.

Verbal arguments

Mathematical ecologists often distrust verbal arguments. They think that such arguments are necessarily fuzzy and can easily give wrong answers. I think that mathematical arguments are as subject to the same failings. A face of precision can be achieved by ignoring the fuzziness of the real world as well as by abstracting the real causal structure. What are now called fuzzy sets (Zadeh, 1965) were first discovered (Van Valen, 1964) because of the imprecision of biological groups. Fuzzy logic remains unpublished as a precise tool for dealing with imprecision. I, at least, find it easier to gloss over assumptions in mathematical arguments than in verbal ones (cf. Lakatos, 1963-1964). A verbal argument can be as tight as a symbolic one; both can be misused. The common prejudice against verbal argument is curious for a subject like ecology whose mathematical foundations are of shifting sand.

Optimization and prediction

It is often assumed that, as Cody (1974) put it, "As all important processes and patterns in biology are products of natural selection, it is somewhat tautologous to speak of optimization in a biological context." But it is far from tautologous; it is often false. There are many mechanisms for nonadaptive and even inadaptive evolution (Van Valen, 1960; cf. also Van Valen, 1974). One adaptation can preclude another for developmental or energetic reasons, optimization at one level of selection can conflict with that at another, chance or historical factors can determine which adaptive peak is climbed, and so on. Examples come easily once one thinks they can, and Cody's statement is more extreme than his thought. Bridges' injunction to geneticists to "treasure your exceptions" applies to optimizers too. It is, moreover, far from a trivial question to ask exactly what natural selection at any one level maximizes. (I believe that the answer from one viewpoint is energy control and from another is nothing at all: cf. Van Valen, 1973b.)

An emphasis on prediction is dangerous when it is made at the expense of attention to the structure of the theory. Contradictory theories often give the same predictions for some phenomena (cf. the three current theories for molecular evolution). If one hasn't thought of all possible alternative theories, prediction is less useful as a test than is investigation of the assumptions and the validity of the deductions from them. Our belief in evolution isn't based on the critical test that Darwin proposed for his (verbal) theory; in fact the test is sufficiently unknown that the supposed unfalsifiability

of the theory has a literature of its own. Darwin noted that if there is any structure of one species that benefits only other species, his theory could not apply. Ghiselin (1969) has discussed other tests that Darwin made. A major reason for our belief in evolution remains its deductive structure (which I have formalized, as of its state in 1838, in unpublished work) and its assumptions from the everyday experience of naturalists. A theory can have more than one derivation and so cannot be disproved by disproving a derivation. For a deductively based theory the situation is the reverse of Popper's paradigm; proof is possible and disproof is not.

Comparison of methods

Verbal and mathematical arguments have different roles in ecological theory. As a general property of the world, causal chains have the same formal structure as many deductive arguments; causation is the image of implication in this mapping. This fundamental relationship is commonly overlooked, but is why parts of mathematics represent the real world dynamically as well as statically, in process as well as in form. The isomorphism resolves in one way a problem which Wigner (1960) called "the empirical law of epistemology," that physical laws are more accurate than the data available when they were formulated. Any function representing a real process can be derived in a manner isomorphic to the causal process it represents. To get dynamic information from an equation or a graph requires at least a short deduction, implicit or explicit; the structure of this deduction is that of the causal process of interest. Moreover, both causation and deductive mathematics can be regarded in two ways. One, the more usual for causation, is as a temporal sequence. The other, now the more usual for mathematics and theoretical physics, is as a timeless, immanent, overall description. The manipulations of mathematics permit knowledge of causal structure that is not apparent from inspection. Symbols can be manipulated more easily than words, so mathematics can tell us what might be true. In ecology, so far, this is all it can do in most cases.

To get beyond the restrictions that the conditions of manipulation impose, we can use words. Some problems are more easily, or (in practice) only, expressible verbally. The evidence bearing on the regulation of trophic levels (Van Valen, 1973a) is of this sort, although May (1973) has given a nice mathematical treatment of the structure of one hypothesis. Words then give us reality but in a clumsy way.

Sometimes the clumsiness can be removed; the conceptual antecedents of the formal theory may then be forgotten. The basic principle of the equilibrium theory of species turnover, applied to island biotas by MacArthur and Wilson (1963), had been developed with minimal quantification by Simpson (1944) and Lyell (1832) for paleontology. (Lyell's estimate or guess of 1 species extinction and origination per year is remarkably close to mine.) Schmalhausen (1946, and even in the bowdlerized 1949 translation) had distinguished the concepts of r and K selection without giving them names. These antecedents do not negate, but give perspective to, the important recent advances.

The translation of mathematics into words (and the converse) is a neglected subject. Such verbal concepts as niche width and intensity of competition do not well reflect their mathematical counterparts. A translation is of course necessary when mathematics is used, but it requires care for both the concepts and the behavior of the symbols. It is not rare to find even undefined symbols, and carelessness with concepts is perhaps the rule.

Additionally, the constraints of mathematics inhibit relaxing these very constraints even where possible. For instance, ultimate regulatory factors of population density are not yet part of mathematical ecology. They come naturally

out of a verbal analysis of reality (Lack, 1954), but their very existence has been questioned by excellent mathematical ecologists because current theory has no place for them. They happen to be at the next level of abstraction from current theory and are mathematically tractable, but the mathematical framework is narrow enough to have prevented their discovery there.

For diversity

A peculiarity of the view that there is only one way to do population biology (or anything else) is the attribution of one's own motives and questions to workers with different approaches. The conclusion is predictable: the other approaches are inferior to one's own. Thus Lewontin (1972) interpreted the classical work of the British ecological geneticists as if they have been trying to prove that natural selection is a predominant evolutionary force; he concluded that they have not done this very well. But the British ecological geneticists don't stop studying a species or character when they find that natural selection is operating on it, as they would if Lewontin's motive were theirs. This is just the beginning. They are interested in the equally basic but very different question of how natural selection in fact operates. They take its importance for granted.

There are different ways to do theory, and each has its limitations. I have not considered such approaches as phenotypic ecology, systems ecology, analytical paleoecology, physiological ecology, and theory resulting from intensive study of organisms as organisms. Each has its advantages, but only what is called mathematical ecology seems to suffer from delusions of omnipotence.

Acknowledgments

I thank J.E. Cohen, J.F. Fox, T.H. Frazzetta, E.G. Leigh, S. Levings, R. Levins, V.C. Maiorana, M. Slatkin, and J.J. Sohn for comments or discussion.

Literature Cited

- Blum, H. 1973. Biological shape and visual science. *Jour. Theor. Biol.* 38: 205-287.
- Bosch, C.A. 1971. Redwoods: a population model. *Science* 172:345-349; 174: 435-436.
- Bruce, D. 1923. Preliminary yield tables for second-growth redwood. *Univ. California Agric. Expt. Sta. Bull.* 361:425-467.
- Cody, M.L. 1974. Optimization in ecology. *Science* 183:1156-1164.
- Fritz, E. 1929. Some popular fallacies concerning California redwoods. *Madroño* 1:221-223.
- Ghiselin, M.T. 1969. *The Triumph of the Darwinian Method*. Berkeley: Univ. California Press. 287 pp.
- Gill, D.E. 1974. Intrinsic rate of increase, saturation density, and competitive ability. II. The evolution of competitive ability. *Amer. Nat.* 108:103-116.
- Jolicoeur, P., and A.A. Heusner. 1971. The allometry equation in the analysis of the standard oxygen consumption and body weight of the white rat. *Biometrics* 27:841-855.
- Lack, D. 1954. *The Natural Regulation of Animal Numbers*. Oxford: Clarendon Press. 343 pp.
- Lakatos, I. 1963-1964. Proofs and refutations. *Brit. Jour. Philos. Sci.* 14:1-25, 120-139, 221-245, 296-342.

- Levins, R. 1966. The strategy of model building in population biology. *Amer. Sci.* 54:421-431.
- Lewontin, R.C. 1972. Testing the theory of natural selection. *Nature* 236: 181-182.
- Lyell, C. 1832. *Principles of Geology*. Ed. 1, vol. 2. London: John Murray. 330 pp.
- Mac Arthur, R.H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39:599-619.
- _____. 1972. *Geographical Ecology*. New York: Harper and Row. 269 pp.
- _____, and E.O. Wilson. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17:373-387.
- May, R.M. 1973. *Stability and Complexity in Model Ecosystems*. Princeton: Princeton Univ. Press. 235 pp.
- Namkoong, G., and J.H. Roberds. 1974. Extinction probabilities and the changing age structure of redwood forests. *Amer. Nat.* 108:355-368.
- Roy, D.F. 1966. Silvical characteristics of redwood (*Sequoia sempervirens* [D. Don] Endl.). U.S. Forest Serv. Res. Pap. PSW-28:1-20.
- Schmalhausen, I.I. 1946. *Faktery Evolyutsii*. Moscow: Izdatel'stvo Akad. Nauk SSSR. 396 pp.
- _____. 1949. *Factors of Evolution*. Philadelphia: Blakiston. 327 pp.
- Simpson, G.G. 1944. *Tempo and Mode in Evolution*. New York: Columbia Univ. Press. 237 pp.
- Vandermeer, J.H. 1973. Generalized models of two species interactions: a graphical analysis. *Ecology* 54:809-818.
- Van Valen, L. 1960. Nonadaptive aspects of evolution. *Amer. Nat.* 94:305-308.
- _____. 1964. An analysis of some taxonomic concepts. In *Form and Strategy in Science* (J.R. Gregg and F.T.C. Harris, eds.), pp. 402-415. Dordrecht, Holland: D. Reidel.
- _____. 1968. Fitness and phenotype in *Drosophila melanogaster*. *Proc. XII Int. Cong. Genet.* 1:230.
- _____. 1973a. Pattern and the balance of nature. *Evol. Theory* 1:31-49.
- _____. 1973b. A new evolutionary law. *Evol. Theory* 1:1-30.
- _____. 1974a. A natural model for the origin of some higher taxa. *Jour. Herpetol.* 8:109-121.
- _____. 1974b. Multivariate structural statistics in natural history. *Jour. Theor. Biol.* 45:235-247; 48:501.
- Wigner, E.P. 1960. The unreasonable effectiveness of mathematics in the natural sciences. *Commun. Pure Appl. Math.* 13:1-14.
- Wright, S. 1921. Systems of mating. *Genetics* 6:111-178.
- Zadeh, L.A. 1965. Fuzzy sets. *Inform. Control* 8:338-353.