

Idealized, inaccurate but successful: A pragmatic approach to evaluating models in theoretical ecology

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Abstract. Ecologists attempt to understand the diversity of life with mathematical models. Often, mathematical models contain simplifying idealizations designed to cope with the blooming, buzzing confusion of the natural world. This strategy frequently issues in models whose predictions are inaccurate. Critics of theoretical ecology argue that only predictively accurate models are successful and contribute to the applied work of conservation biologists. Hence, they think that much of the mathematical work of ecologists is poor science. Against this view, I argue that model building is successful even when models are predictively inaccurate for at least three reasons: models allow scientists to explore the possible behaviors of ecological systems; models give scientists simplified means by which they can investigate more complex systems by determining how the more complex system deviates from the simpler model; and models give scientists conceptual frameworks through which they can conduct experiments and fieldwork. Critics often mistake the purposes of model building, and once we recognize this, we can see their complaints are unjustified. Even though models in ecology are not always accurate in their assumptions and predictions, they still contribute to successful science.

Keywords: accuracy, ecology, heuristic, idealization, mathematics, model, pragmatism, prediction, theory

Introduction

In this essay, I explore how simple models in theoretical ecology can be used to investigate and learn about complex populations, communities, and ecosystems. There are *prima facie* difficulties with using simple models to uncover the patterns and mechanisms of populations and communities, which many philosophers and ecologists have drawn our attention to. Most models in ecology are highly idealized; the systems the models represent are often quite complex. Thus, estimating the parameters and variables of the models so they can be experimentally tested can be extremely difficult. If models are idealized and are hard to test, then how can theory based on these models be successful, and how do we evaluate their purported success? Critics have argued that if model building is to be a successful part of ecology, especially applied ecology, then these mathematical models must be predictively accurate. Predictive inaccuracy here has been construed in a broad sense: mathematical models are not predictively accurate when they issue no predictions, cannot be tested, or fail their respective tests (see Shrader-Frechette and McCoy 1993, Peters 1991, Simberloff 1983, and Strong 1983).

I argue for a pragmatic approach in understanding the success and evaluation of ecological modeling.¹ On my view, model building is first and foremost a *strategy* for coping with an extraordinarily complex world. In order to understand the role of models in ecology, one must understand what models are used to do and what the aims of theoretical ecology are. First, I consider the worries of the critics and will attempt to

¹ See Boyd and Richerson 1987, Caswell 1988, Cooper 1990, Levin 1980, 1981, May 1981, Pielou 1981, Roughgarden 1984, and Wimsatt 1987 for similar approaches. For a philosophical account of science that emphasizes the strategies of science, models and representation, and a sensible realism, see Godfrey-Smith 2003.

show how we can dispel some of the current skepticism. Second, I will sketch several important uses of models in theoretical ecology. Critics often mistake what the purposes of model building are and hence what it can accomplish. If the sole aim of model building in theoretical ecology was predictive accuracy, then their worries might give us pause. However, once we recognize that mathematical models are used for a variety of purposes, we can see that the critics' complaints are unjustified. Finally, I respond to a worry about the "theories as tools" approach offered by Daniel Simberloff.

Models and idealizations

I will focus on mathematical models in ecology, though not all ecological models are mathematical (Downes 1992, Griesemer 1990). We can represent these models with deductively closed sets of assumptions. As an example, x is a Lotka-Volterra predator-prey system if, and only if, x obeys the laws of succession

$$\begin{aligned}dV / dt &= rV - aVP \\dP / dt &= baVP - qP\end{aligned}$$

where V and P are the prey and predator abundances respectively, a is the capture efficiency of the predator, b is the conversion efficiency of predator, r is the intrinsic rate of increase of the prey, and q is the mortality rate of the predator.² We can formulate theoretical hypotheses concerning models and empirical systems. For instance, we might claim that some of a model's particular assumptions or predictions accurately represent certain aspects of a given empirical system.

² When modelers and mathematicians refer to laws of "succession", they are referring to the rules governing how the states of the system succeed one another with respect to time. They are not referring to the phenomena of ecological succession. Thanks to an anonymous reviewer for noticing the bit of potentially confusing terminology.

It is a truism amongst ecologists that mathematical models in their science are idealized. A theory or model is idealized only if the theory or model is an *inaccurate* representation of the system of interest. Specifically, a theory or model is idealized only if the theory or model has some false assumption(s).³ For example, in some evolutionary models, random genetic drift is ignored and populations are assumed to be effectively infinite in size. This assumption can ensure that expected reproductive success and actual reproductive success of some type of organism are one and the same. It is in virtue of ignoring the role of drift that some selection models are idealized.

Idealizations are false assumptions of models. However, this is necessary but not sufficient for an assumption to be an idealization. If idealizations were just false assumptions of theories or models, then all false models or theories would be idealized. It would be reasonable then for a scientist to always argue that a useless, false model or theory was just idealized. Clearly though, some theories or models are not idealized per se but are dead ends. I suggest that a necessary and sufficient criterion for an assumption to be an idealization is the following: An assumption is idealized just in case the assumption is *false* and it is *useful* for some purpose to scientists. Moreover, a model is idealized just in case it has at least one idealized assumption.⁴

Ecological systems and their properties are extremely difficult to measure and

³ Assumptions of models concern features of the following form (Bender 1978, 4): (1) the choice of state variables, (2) the choice of parameters—constant values or random variables, and (3) the choice of the mathematical form of the laws of succession and coexistence—continuous or discrete, deterministic or stochastic. In the construction of models, modelers make particular assumptions about the dynamical systems they are working with. However, these assumptions all come in one of these forms. What makes an assumption different from a prediction? Predictions are claims made about the values or configuration of the state variables. The three types of assumptions above do not concern the values or configuration of the state variables but rather reflect the *choice* of the state variables, parameters, and the mathematical form of the laws of the model.

⁴ As a consequence of my definition of ‘idealization’, it is true that many what are sometimes called “data models” contain idealizations as well. For example, the species abundance models—broken-stick, geometric, and lognormal, etc.—of community ecology are data models but are idealized.

estimate for several reasons (Brandon 1993). Three of the most important are worth pointing out. First, most time frames for adequate ecological fieldwork and experiments are significantly longer than the time available for ecologists to conduct their studies (Pimm 1992). This results in part from the fact that research grants are typically given for relatively short time periods but ultimately it means that ecologists must conduct their studies on relatively small time scales (10 years or less).

Second, it is extremely difficult to manipulate ecological systems in systematic and controlled ways. There are multifarious factors at work and only some of them are recognized at any given time. Third, for those systems that can be manipulated, it is often unclear how they are relevant to systems that cannot be manipulated. For example, G. F. Gause (1935) argued that species of *Paramecia* obeyed the competitive exclusion principle as the Lotka-Volterra interspecific competition model suggests. When *P. aurelia* and *P. caudata* were grown in a mixed culture, *P. aurelia* excluded *P. caudata*. Nonetheless, there is serious doubt concerning the relevance of these systems and their behavior to other non-laboratory systems. Laws of succession and coexistence may be true of some empirical systems but may only apply to very contrived systems designed to fit the equations of a model (Cartwright 1995). The exportability of scientific knowledge generated in “bottle experiments” is controversial. If the time frames of ecological experiments are very short and the ecological systems of interest are difficult to experiment on, then it is remarkably hard to reliably estimate or measure the parameters of complex models.

Before I turn to the different uses of models, consider the worries of the critics of model building (Peters 1991, Shrader-Frechette and McCoy 1993, Simberloff 1983, and

Strong 1983). We have seen that some mathematical models are highly idealized. It is difficult to estimate the parameters of these models since the relevant time frames for conducting suitable empirical studies are much longer than those ecologists have available to them; ecological populations and communities are very difficult to manipulate experimentally; and the circumstances in which models can be tested against laboratory populations are not obviously relevant to natural populations or communities. Hence, it is very difficult to test these models as well.

The critics' argument says that if model building in theoretical ecology is to be successful, and ultimately of use to conservation biologists, then surely these models must be predictively accurate. However, models in ecology are often predictively inaccurate: they do not issue predictions, those predictions are untestable, or the testable predictions are dramatically false (Peters 1991, 17-73, 178-219, Shrader-Frechette and McCoy 1993, 11-79). It follows, say the critics, that models are not a successful part of ecology. As Daniel Simberloff (1981) writes,

Ecology is awash in all manner of untested (and often untestable) models, most claiming to be heuristic, many simple elaborations of earlier untested models. Entire journals are devoted to such work, and are as remote from biological reality as are faith-healers.

Ecologist R. H. Peters writes,

If scientific theories are characterized by predictive ability, the branches of science are distinguished by the objects of prediction. Ecology seeks to predict the abundances, distributions and other characteristics of organisms in nature.... This book contends that much of contemporary ecology predicts neither the characteristics of organisms nor much of anything else. Therefore it represents neither ecological nor more general scientific knowledge (1991, 17)

Different critics recommend different ways of coping with the predictive failure of models. Peters (1991) argues that since predictive accuracy is *the* goal of science and

should be the goal of ecology, then we should dismiss or severely reduce the activity of traditional model building. Shrader-Frechette and McCoy (1993) argue that modeling should be replaced with case studies that embody local natural history and autoecology. Last, ecologists Daniel Simberloff (1983) and Donald Strong (1983) argue that ecologists should be slow to model processes (such as interspecific competition), or at least to apply models, unless it has been shown that the relevant null hypothesis is false and some process to be modeled is in operation. To do otherwise, they argue, is a poor use of intellectual resources and a departure from a proper Popperian philosophy of science.

Even without delving into the details of these particular proposals we can see serious problems with the previous argument. First, many ecological models can accurately represent some empirical systems in their fit to the phenomena. We must also remember that claims of predictive accuracy are best construed as *contextual* claims. That is, any claim about a model's predictive accuracy is relative to three considerations (see Giere 1988, 1999):

- (a) the *respects* in which the model is meant to be an accurate representation,
- (b) the *degree* to which those respects are supposed to accurately represent phenomena, and
- (c) the *system* of which the model is supposed to be an accurate representation.

Moreover, if one writes that a model's prediction is *false*, we should take this to mean that the prediction does not fit the phenomena sufficiently well. The notion of "sufficient fit" is specified via the context mentioned above and through statistical methodology. Second, the argument assumes that the most important function of models is to provide empirically accurate predictions. However, as I will argue in the next section, models are used to do a variety of things that do not involve the goal of predictive accuracy. In fact, models can perform those functions *even when they are predictively inaccurate and are*

thoroughly idealized. We must evaluate models for performing the tasks that they are designed for.

Shrader-Frechette and McCoy grant, unlike Peters, that models might provide the basis for the construction of theory for environmental problem-solving advice. They write

...Peters is wrong to use prediction as a *criterion for*, rather than a *goal of*, ecological theorizing, because not all sciences are equally predictive... In overemphasizing the importance of *prediction* in ecology and science generally, Peters has erred in underemphasizing the role of *explanation* (1993, 109).

There are several problems with this auxiliary argument. First, I will argue that there are several purposes models in ecology fulfill which do not depend on models being either predictively accurate *or* explanatory. In some cases, of course, models may be explanatory. For example, if on the basis of a mathematical model, some ecologist offers a how-possibly explanation, then my account of model functions and an account of explanation may overlap. However, they need not. On the basis of a model, we may *explore* chaotic dynamics without that model thereby *explaining* a time series of some population. Hence, if Shrader-Frechette and McCoy are arguing that model building in ecology is successful only if mathematical models are either predictively accurate or explanatory, then this would be false as well. At the very least, Shrader-Frechette and McCoy would have to show that the only functions of mathematical models in ecology are predictive accuracy and explanation. We may ask, however, whether predictive accuracy is the only function of mathematical modeling in ecology. As a way to take up this question, let us now consider what models are used for in theoretical ecology.

A pragmatic approach to models or what are models for?

Models are used for at least four basic purposes in theoretical ecology.⁵

- 1) Models are used to *explore possibilities*.
- 2) Models give scientists simplified means by which they can *investigate more complex systems*.
- 3) Models provide scientists with *conceptual frameworks*.
- 4) Models can be used to generate *accurate predictions*.
- 5) Models can be used to generate *explanations*.

I will sketch the first three of these functions with examples from population and community ecology since they are often ignored in philosophical discussions of models, though I do think models in ecology do satisfy the goal of predictive accuracy and explanation in many cases.⁶

Exploring Possibilities

One of the ways in which models contribute to ecologists' understanding of the biological world is through the exploration of possibilities (Cooper 1990). Often models are tools that help biologists recognize possible relations between natural phenomena by tracking relationships between variables and parameters in models. They form the basis for theoretical hypotheses as to what ecological systems *would do* under certain circumstances. For example, philosopher of biology Robert Brandon has argued that evolutionary models provide the basis for "how-possibly" explanations (Brandon 1991).

An example in ecology of this model function comes from the work of Robert May (1973, 1974, 1975, 1976; May and Oster 1976). May demonstrated that very simple models of ecological systems could lead to chaotic behavior where a dynamical system

⁵ I do not mean to suggest that this list is exclusive or exhaustive. However, in reviewing the literature, these model functions are particularly apparent. It should also be said that a single model could perform several of these functions at once and at different moments in time.

⁶ See Morgan and Morrison 1999, for an interesting discussion of "models as mediators" that is similar to the analysis I carry out here. However, contrary to their view, nothing I say here is inconsistent with the semantic view of theories.

exhibits chaos if it is extremely sensitive to initial conditions and if its behavior is unstable and aperiodic. May investigated many different models; however, some of the simplest were discrete difference equations.

Consider the following discrete logistic equation:

$$N_{t+1} = N_t + N_t R \left(1 - \frac{N_t}{K} \right)$$

May demonstrated that some very interesting behavior would arise for various values of R , the parameter that describes the population's per capita rate of increase. He found that for values of $R \leq 2.57$, the model population would exhibit stable equilibria and stable cycles. However, if the values of $R > 2.57$, then there are no stable equilibria or cycles, and with other assumptions met, the population exhibits a bewildering array of unstable, aperiodic behavior.⁷

It is the subject of current research whether ecological systems are chaotic and how ecologists might determine if they are (Hastings et. al. 1987; Cushing et. al. 2003). This, however, is a very challenging undertaking. To see the difficulties involved, suppose we have a dynamical system that is chaotic and we are trying to determine some future state $N(t + m)$ where $m > 0$. Normally, one would determine the initial conditions of the system and enter the values of the parameters R and K in the discrete logistic and recursively determine the future state. However, if the system is chaotic, it will exhibit extreme sensitivity to initial conditions and will be unstable and aperiodic. If these conditions are met, then slight variations in those conditions can lead to extremely different dynamics. Unfortunately, we cannot discriminate on the basis of the data what

⁷ The model is patently idealized. One reason for this is that the population size can become negative if $N_t > K(1 + R)/R$ (May 1974, 645).

the actual initial conditions are and will only be able to approximate them. The measurement error involved in such estimation will “hide” the actual initial conditions. Hence, it may be impossible to predict the state of the system at $t + m$.

Researchers have been analyzing time series to assess the degree to which such systems are density dependent and sensitive to initial conditions. One way of quantifying this sensitivity is through a measure called a *Liapunov exponent*. Suppose we have an initial population of size N_0 and consider a nearby population of size $N_0 + \Delta_0$, where Δ_0 is very small. After n time steps we can examine the sizes of two respective populations, the first starting at N_0 and the second at $N_0 + \Delta_0$. Let $|\Delta_n|$ be the absolute value of their difference. We can do this again and again for n different time steps and then fit this data to an exponential model with an elapsed time of n as the independent variable, such that:

$$|\Delta_n| = |\Delta_0| e^{n\lambda}$$

This resulting model has one parameter, the *Liapunov exponent* λ (Case 2000, 116-117). If $\lambda < 0$, then populations are converging on the same pattern as time goes by; if $\lambda > 0$, then the difference between populations at the initial times is growing exponentially over time and this is indicative of chaos.

Even if we suppose that this current research will not demonstrate whether chaos is present in any particular ecological system, the importance of May’s work is still clear: it counsels that ecologists ought to pay more attention to nonlinear, unstable, aperiodic behavior. May writes,

That simple models can do complicated things is not a new idea: Poincaré expressed despair of ever completely understanding the motions of even trivial mechanical systems. Nevertheless, there is still a tendency on the part of most ecologists to interpret apparently erratic data as either stochastic “noise” or random experimental error. There is, however, a third alternative, namely, that

wide classes of deterministic models can give rise to apparently chaotic dynamical behavior. It is this third possibility which we elaborate in this paper (May and Oster 1976, 573).

Here we see May concluding that ecologists have been unjustified in assuming that “noisy” phenomena are the result of either stochasticity or measurement error alone, and that it is *possible* that the same phenomena are the result of deterministic chaos.

This is especially important given the debates among population ecologists over population regulation. The *biotic school* as developed by Howard and Fiske (1911), Nicholson (1933), and Smith (1935) argued that populations are regulated primarily by factors that depend on their density. The population will increase when low and will decrease when high and thus average population densities remain stationary. The *climatic school* pioneered by Bodenheimer (1931) and most forcefully by Andrewartha and Birch (1954) argued that populations are driven by changes in the environment like weather and thus fluctuate greatly. Thus, it appears we have a crucial test of the two schools: if population densities are stationary, then the biotic school is correct; if population densities are wildly fluctuating, then the climatic school is correct. May argues this is fundamentally wrongheaded.

These studies of the Logistic Map revolutionized ecologists’ understanding of the fluctuations of animal populations... With the insights of the Logistic Map, it was clear that the Nicholson-Birch controversy was misconceived. Both parties missed the point: population-density effects can, if sufficiently strong..., look identical to the effect of external disturbances. The problem is not to decide whether populations are regulated by density-dependent effects (and therefore steady) or whether they are governed by external noise and therefore fluctuate). It’s not a question of either/or. Rather, when ecologists observe a fluctuating population, they have to find out whether the fluctuations are caused by external environmental events (for example, erratic changes in temperature or rainfall), or by its own inherent chaotic dynamics, as expressed in the underlying deterministic equation that governs the population’s development (May 2002, 39-40)

Mathematical modeling allows ecologists to explore possibilities.

“Ridiculous” Models as Baselines

Models also allow scientists to investigate systems that are more complex than the model used. Scientists often employ models that clearly do not display a statistically significant goodness-of-fit to the phenomena. Nonetheless, these models serve as a ‘baseline’ for recognizing the important ways in which more complex phenomena deviate from these simpler representations. One case of this sort concerns the adaptationism debate in behavioral and evolutionary ecology. Biologists often use optimality models in which it is assumed that natural selection is the only important force of evolutionary change. They recognize that selection is not the only operative mechanism in natural systems, but simplifying in this way allows them to compare expected behaviors of the model systems with those more complex natural systems that include other evolutionary forces such as mutation, genetic drift, and inbreeding. By virtue of this comparison, biologists can determine how and to what degree the actual system under consideration deviates from the optimality models and what constraints to take into consideration (see Orzack and Sober 1993). As Elliott Sober writes,

Adaptationalist thinking is an indispensable research tool. The only way to find out whether an organism is imperfectly adapted is to describe what it would look like if it were perfectly adapted (1996[1998], 83).

There are several different ways in which “false models lead to truer theories” (Wimsatt 1987). Generally, if the predicted consequences of the equations with initial conditions are sufficiently different from the data describing the behavior of the population or community, then the theoretical hypothesis that the model and the phenomena exhibit a good fit is inadequate. It is then crucial to move from the fact that they are dissimilar in this respect to localizing the error in the hypothesis. Systematically

investigating the error will force one to reject some assumption of the model or the model completely (or the initial conditions or auxiliary hypotheses). It might be the case that we have left out relevant variables that are needed to describe the dynamics of the empirical system or we may have misdescribed the relations between the state variables in the laws of the model. We may have ignored important parameters that drive the system and so on. In this sense, ecologists must minimally be concerned with the realism of their models' assumptions and with biases in their model building (Hausman 1992, Wimsatt 1980). In order to improve the empirical accuracy of our models, we must determine which assumptions are at fault.

Predator-prey theory is a good example of how we can use simple models to better understand complex systems. In fact, by examining how the simplest model fails in accurately representing predator-prey systems, ecologists have articulated a sophisticated repertoire of more realistic models.⁸ As we have seen in the simplest Lotka-Volterra predator-prey system, we have coupled differential equations, one describing the instantaneous rate of change in prey abundance and the other describing the instantaneous rate of change in predator abundance.

All classical predator-prey models are of the following form.

$$\frac{dV}{dt} = \left(\begin{array}{l} \text{growth rate of the prey} \\ \text{population in the absence} \\ \text{of the predator} \end{array} \right) - \left(\begin{array}{l} \text{capture rate of} \\ \text{prey per} \\ \text{predator} \end{array} \right) P$$

$$\frac{dP}{dt} = \left(\begin{array}{l} \text{rate at which each predator} \\ \text{converts captured prey into} \\ \text{predator births} \end{array} \right) - \left(\begin{array}{l} \text{rate that predators} \\ \text{die in absence of} \\ \text{prey} \end{array} \right) P$$

⁸ The following discussion of predator-prey models comes from J. Roughgarden (1979, 432-451).

In the simplest model of a predator-prey system, we assume that (a) the prey grows exponentially in the absence of the prey (rV), (b) predator and prey encounter one another randomly in proportion to the abundance (VP), (c) the predators have a linear functional response (aV), (d) the numerical response of the predator is a constant multiplied by the functional response [$b(aV)$], and (e) the predator declines exponentially in the absence of the prey (qV). This gives us the following model.

$$\begin{aligned}\frac{dV}{dt} &= rV - aVP \\ \frac{dP}{dt} &= baVP - qP\end{aligned}$$

At equilibrium $dV/dt = dP/dt = 0$, and so we have

$$V^* = \frac{q}{ab}$$

$$P^* = \frac{r}{a}$$

The prey equilibrium V^* is determined by properties of the predator. Likewise, the predator equilibrium P^* is determined by the properties of the prey. This general feature is present in all classical predator-prey models.

The simplest Lotka-Volterra model exhibits mathematically interesting dynamics. The equilibria of the model are not locally asymptotically stable, but this model does not exhibit unstable behavior either. A numerical analysis of the model reflects the fact that solutions to the equations are cycles, where the amplitude of the cycle is completely determined by the initial conditions. This is called *neutral stability*. So, if the system

starts with a large-amplitude cycle, it will continue in such a cycle indefinitely. The same is true of a small-amplitude cycle as well. We can see this from Figure 1.

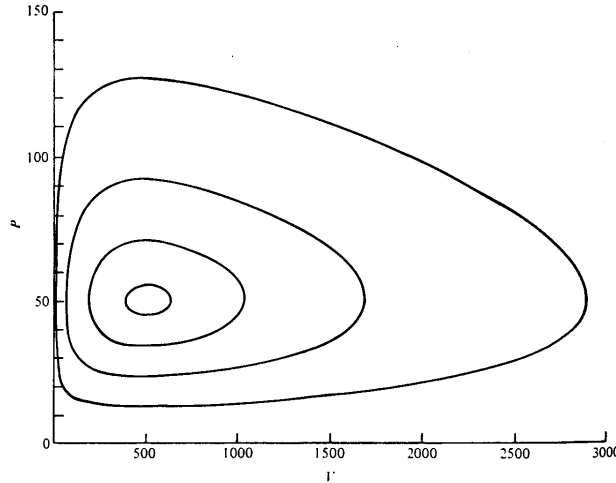


Figure 1. A phase portrait of the Lotka-Volterra predator-prey model exhibiting neutral stability (taken from Roughgarden (1979)).

Ecologists consider the Lotka-Volterra predator-prey model to be unrealistic, since a small change in the initial conditions can lead to large changes in the oscillations exhibited by the model. Natural predator-prey systems could never exist if they were so vulnerable to small changes. It is by recognizing this important empirical deficiency of the simplest Lotka-Volterra predator prey model that we can better understand the dynamics of these interacting populations.

It is apparent that Alfred Lotka himself recognized this point. In his *Elements of Mathematical Biology*, he writes regarding the parameter a (or k in his notation),

Regarding the function k , we shall make the very broad assumptions that it can be expanded as power series in N_1 and N_2 , thus $k = \alpha + \beta N_1 + \gamma N_2 \dots$. Nonetheless, it will be convenient first of all to consider an approximation (1956, 88-9).

That is, he assumes the functional response has an extremely simple form and thus one has the classic Lotka-Volterra predator prey model. He claims (independent of

observations) that when one takes into account the second and higher degree terms, then one gets a “damped oscillation” (1956, 92). Of course, he did not show this but sends the reader to the original literature and a paper by Henri Poincaré!⁹

One way of inducing stability in our Lotka-Volterra predator-prey model is to assume that our prey does not grow at an exponential rate of (rV) in the absence of the predator. Rather, we assume that the prey grows at a logistic rate of $dV/dt = rV(1 - V/K)$ in the absence of the predator where K is the carrying capacity of the prey. Thus, our revised model is

$$\begin{aligned}\frac{dV}{dt} &= rV\left(1 - \frac{V}{K}\right) - aVP \\ \frac{dP}{dt} &= baVP - qP\end{aligned}$$

We should recognize first that at equilibrium $dV/dt = dP/dt = 0$, the predator’s abundance is still determined by the properties of the prey and the prey’s abundance is still determined by the properties of the predator since

$$V^* = \frac{q}{ab}$$

$$P^* = \frac{r}{a}\left(1 - \frac{V^*}{K}\right) = \frac{r}{a}\left(1 - \frac{q}{abK}\right)$$

⁹ Vito Volterra (1926) takes a different attitude towards neutral stability. First, he claims that there are three “laws” that can be deduced from the model (1926, 558-9). First, the fluctuation of the species is periodic depending only on initial conditions. Second, the average numbers of the two species tend to have constant values. Third, he states what we now call the “Volterra Principle”—anything that both increases predator mortality and decreases the rate of growth of prey will lead to an increase in the prey abundance and a decrease in the predator abundance. Volterra then claims that the third law “is undoubtedly the most interesting of all, because it affords the best actual verification so far found of the theory” (1926, 284). This is particularly interesting because confirmation of the Volterra Principle provides next to no confirmation of the first two laws since all of the classical predator prey models obey the Volterra Principle and only the simplest possesses neutral stability.

The only difference from the previous model is the logistic term in the prey's growth equation, which now includes the carrying capacity of the prey. We thus can avoid the deficiency of the previous model by incorporating an ignored parameter K —the carrying capacity of the prey population.

The logistic predator-prey model generates more realistic oscillatory behavior. Applying a local stability analysis to our model, we can determine that the equilibrium is stabilized by adding density-dependence to the prey's rate of growth in the absence of the predator. This is shown graphically in Figure 2.

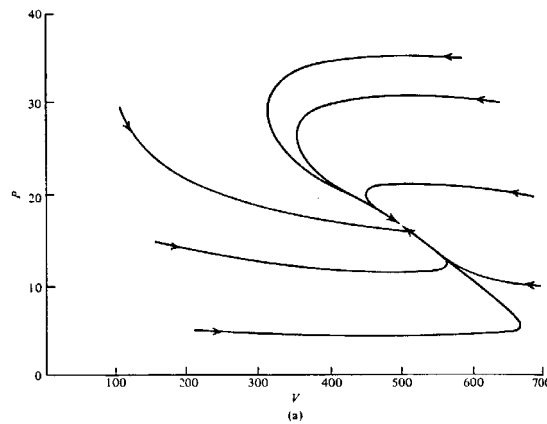


Figure 2. A phase portrait of the predator-prey model with logistic growth of the prey in the absence of the predator ($r = 0.5$, $a = 0.01$, $b = 0.02$, and $K = 750$). Here the carrying capacity of the prey is very low and thus the stable equilibrium is approached without oscillations (taken from Roughgarden (1979, 442))

This stable equilibrium can still be approached in an oscillatory fashion, however, depending on the value of K . This can be seen in Figure 3.

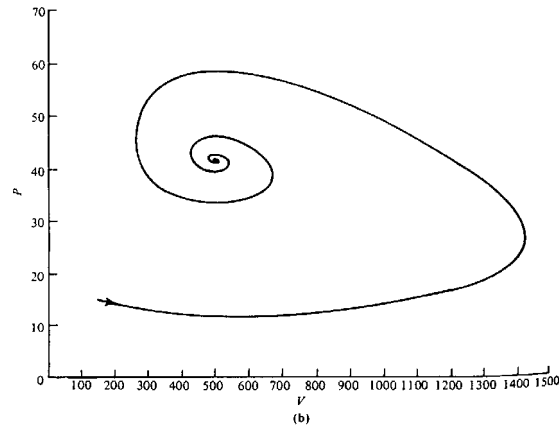


Figure 3. A phase portrait of the predator-prey model with logistic growth of prey in the absence of the predator ($r = 0.5$, $a = 0.01$, $b = 0.02$, $d = 0.1$, and $K = 3000$). Here the carrying capacity of the prey is relatively high and the stable equilibrium is approached with oscillations (taken from Roughgarden (1979, 442)).

We could also incorporate other ignored biological details like predator satiation when the prey is abundant. If we let c represent the maximum rate of prey capture per predator and a represent how easily a predator is satiated with prey, then one functional response curve that includes satiation is $c(1 - e^{-aV/c})$.¹⁰ Our new predator-prey model is

$$\frac{dV}{dt} = rV \left(1 - \frac{V}{K} \right) - c(1 - e^{-aV/c})P$$

$$\frac{dP}{dt} = bc(1 - e^{-aV/c})P - aP$$

This would give us stable limit cycles (Roughgarden 1979, 443-446). A stable limit cycle

¹⁰ As an anonymous reviewer notes, this is not the most common way to model functional response. More commonly, with h as parameter measuring the handling time per prey item, a Type I functional response is $f(N) = cN$. A Type II functional response is $f(N) = cN/(1 + hcN)$. Finally, Type III functional response is $f(N) = cN^2/(1 + hcN^2)$.

occurs only if for any arbitrarily small perturbation away from the cycle, the system will return to the cycle with the same amplitude and frequency. We can see this from Figure 4.

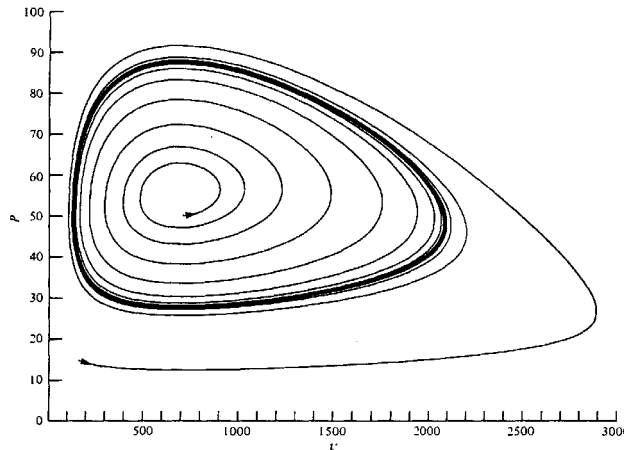


Figure 4. A phase portrait of the predator-prey model with logistic growth of the prey in the absence of the predator and predator saturation ($r = 0.5$, $a = 0.01$, $b = 0.02$, $d = 0.1$, $K = 2500$, and $c = 10$). The stable limit cycle is a “closed orbit” that other nearby trajectories will approach (taken from Roughgarden (1979, 445)).

Thus, this behavior is neither the neutral stability exhibited by the first model nor a stable equilibrium point exhibited by the second model. However, the logistic predator-prey model with predator satiation can exhibit a stable equilibrium point for certain values of K .¹¹

Thus, models with biologically unrealistic assumptions and dynamics like our simplest Lotka-Volterra predator-prey model can teach ecologists important lessons especially when compared with more realistic models. As Richard Boyd and Peter Richerson write,

¹¹ If $K < K_0$, then the predator-prey system has a stable equilibrium point. However, if $K \geq K_0$, then the predator-prey system exhibits stable limit cycles. Technically, K_0 is that value of K at which the system bifurcates from one dynamical behavior to another—mathematically, this property is known as a *Hopf bifurcation*.

A well understood simple sample theory serves as a useful point of comparison for the results of more complex alternatives, even when some conclusions are utterly ridiculous...[M]odels do not usually fail; they fail for particular reasons that are often very informative. Just what modifications are required to make the initially ridiculous results more nearly reasonable? (1987, 41)¹²

We have now seen how we can systematically alter models to replace assumptions that seem grossly implausible with ones that are more plausible given the empirical systems we want to study. In so doing it is possible to explore the dynamics of the models to see how models with different assumptions behave. If we can systematically investigate the various assumptions of the model, then we have a fallible but justifiable way of locating error and revising our hypotheses.

Conceptual Frameworks and Models

Models also provide ecologists with conceptual frameworks by which they can pose questions and carry out experimental investigations. Often models can provide concepts, which can be used independently of the models and can raise important questions. These concepts may correspond to various natural kinds or properties that are causally salient. Ultimately, the concepts outstrip the application of the model and have lives that are independent of their mathematical counterparts and directly contribute to experimental research (Cooper 1993). A case in point concerns debates over the “balance of nature” and the relationship between the complexity and stability of communities.

Robert May (1972) was one of the first ecologists to explore the connections between complexity and stability within the mathematical framework of dynamical

¹² It is important to note though that just because a model is more idealized than another does not mean that the latter is necessarily more accurate predictively than the former. Sometimes idealizing assumptions, which describe the main effects of a causal factor, are better than more detailed assumptions concerning that factor. Ironically, the idealizations do less to distort the models as a whole. Thanks to Nancy Cartwright on this point.

systems—in particular with what are known as “local stability analyses”.¹³ May assumes that we have m species described by the following nonlinear first-order differential equations:

$$dN_i(t)/dt = F_i(N_1(t), N_2(t), \dots, N_m(t))$$

The equilibrium for a species i , denoted as N_i^* , occurs when the number of individuals in the species does not change. Mathematically, this occurs when $dN_i(t)/dt = 0$ and we can find this equilibrium by “solving” the relevant equations.¹⁴ May was interested in what would happen to the community equilibrium when perturbed in a relatively small way. Would the community return to its pre-perturbation equilibrium? To answer this question, we need an expression summing those equilibria and the perturbations. So, we write,

$$N_i(t) = N_i^* + x_i(t)$$

where $x_i(t)$ refers to arbitrarily small changes to the equilibrium N_i^* . In effect, we are taking the equilibrium for each species and perturbing it by the amount $x_i(t)$. Rearranging, we have an equation for the perturbations themselves – it is the new density after the perturbation minus the previous equilibrium.

$$x_i(t) = N_i(t) - N_i^*$$

From a mathematical point of view, things can get exceedingly complex when we try to

¹³ Ecologist Richard Levins (1968) recognized that community interactions could be described by what he called a “community matrix.” One should also see Gardner and Ashby (1970) for a more general exploration of complexity and stability in complex systems.

¹⁴ Ecologists are not interested in just any equilibrium—they are particularly interested in *feasible* equilibria where an equilibrium is feasible if $dN_i(t)/dt = 0$ and $N_i^* > 0$ for all i . In other words, a feasible equilibrium for a community occurs when the rate of growth of each species is not changing *and* all the species are present in the community. If there are no individuals of a given species in a community, then trivially the rate of change is zero.

discover what will happen to the perturbed equilibrium of the community. *However*, if we assume those perturbations are small and do not take us very far from the community equilibrium, then we can provide a linear approximation of the function that describes what happens to $x_i(t)$ through time. Using these techniques and his assumptions about differential equations the community obeys, May arrived at a set of m linear first-order differential equations describing the dynamics of the perturbation itself.

$$\frac{dx_i(t)}{dt} = \sum_{j=1}^m a_{ij} x_j(t)$$

The parameter a_{ij} is the interaction coefficient between species i and j , which represents the effect of the species j on species i . So, if i is a predator and j is prey, then $a_{ij} > 0$ and $a_{ji} < 0$. Similarly, if i and j are competitors, then $a_{ij} < 0$ and $a_{ji} < 0$. If i and j are mutualists, then $a_{ij} > 0$ and $a_{ji} > 0$, and so on. It is also possible that for some species i and j , $a_{ij} = 0$. Interestingly, we can describe the possible interactions among species by the signs of a_{ij} and this is commonly done in ecology textbooks. We can also represent this last equation much more concisely with matrix algebra

$$\frac{d\mathbf{x}(t)}{dt} = \mathbf{A}\mathbf{x}(t)$$

where \mathbf{x} is the $m \times 1$ column vector of x_i and \mathbf{A} is the $m \times m$ “community matrix” or whose elements a_{ij} describe the effect of species j on species i near equilibrium N^* .¹⁵ In effect, \mathbf{x} is a “list” of the perturbations and \mathbf{A} describes how each species affects each other. Matrix algebra allows us to represent and analyze this large set of equations and its properties in an extremely economical fashion. Moreover, it provides us with a concise

¹⁵ Technically, $a_{ij} = (\partial F_i / \partial N_j)^*$.

statement of when an equilibrium will be stable or unstable. An equilibrium point is *locally stable* just in case all of the eigenvalues of the community matrix \mathbf{A} have negative real parts; otherwise, it is unstable. Eigenvalues are special solutions of matrices and as such have no easy explanation – sometimes they involve complex numbers making them even harder to grasp (and thus we talk of eigenvalues having real and imaginary “parts”). Nonetheless, the fundamental point of the analysis above is this: If the community equilibrium we started with is unstable, then the difference between $N_i(t)$ and $N_i^*(t)$ grows with time; if the equilibrium is stable, then the difference shrinks with time and we return to that state.

May modeled his communities with m species and chose the interaction coefficients a_{ij} at random with one sort of exception. He assumed that for each species there was density-dependence or intraspecific competition and hence the diagonal elements of the community matrix – those entries a_{ij} where $i = j$ were negative.¹⁶ Ignoring then the diagonal elements of the matrix, some species interaction coefficients were greater than zero, some less than zero, and some were equal to zero. He defined the *connectance* C of a community to be the proportion of interspecific interactions not equal to zero— $a_{ij} \neq 0$. Finally, the intensity s of the interspecific interaction was a random variable with a mean of zero and a variance of s^2 .

May proved that a model community is “almost certainly” stable if, and only if,

$$s(mC)^{1/2} < 1$$

Therefore, all else being equal, an increase in the number of species m , connectance C , or

¹⁶ The diagonal elements of a $n \times n$ matrix are $a_{11}, a_{22}, \dots, a_{nn}$. These reflect the effect of species i on itself. By assuming that these terms are negative we are assuming individuals of the same species compete.

interaction strength s will lead to a decrease in the stability of a community. This result was truly astonishing. For example, if we hold connectance and intensity of the interactions constant and increase S , then the community will become unstable. This was contrary to what ecologists such as Charles Elton and Robert MacArthur at least appeared to have hypothesized. Moreover, it seemed to fly in the face of conservationist folk wisdom. As Barry Commoner wrote in his 1972 book *The Closing Circle*,

The amount of stress which an ecosystem can absorb before it is driven to collapse is also a result of its various interconnections and their relative speeds of response. The more complex the ecosystem, the more successfully it can resist a stress . . . Like a net, in which each knot is connected to others by several strands, such a fabric can resist collapse better than a simple, unbranched circle of threads—which if cut anywhere breaks down as a whole.

As with most models, “May’s theorem” has been criticized especially with respect to the various simplifications that his model employs. For example, Donald DeAngelis (1975) argued that May’s models were biologically unrealistic and one such reason concerned *donor-dependence*. If a species j is eaten by a species i , then donor-dependence occurs if $\partial F_{ij}/\partial N_j > \partial F_{ij}/\partial N_i$ —in other words, the predator’s dynamics are determined more by changes in the prey’s density than in the predator’s density. DeAngelis noted that donor-dependence can generate stable communities when coupled with other more realistic assumptions. Larry Lawlor noted that randomly constructed communities will contain prey-less predators and predator-less prey, which is biologically unrealistic. Moreover, randomly constructed food webs contain loops where species i feeds on species j , j feeds on species k , and k feeds on i , which is also biologically unrealistic (Lawlor 1978).¹⁷ Note also that there is a sharp transition from

¹⁷ Though some biologists debate this point. One might wonder why Lawlor would criticize May’s model if he did not believe it was predictive. Here is what Lawlor writes, “If May’s conclusions are to be relevant to

stability to instability as described by (4) and that this does not hold for more realistic models.¹⁸

Stuart Pimm (1979) investigated larger perturbations than the arbitrarily small ones of May's analysis on the grounds that the arbitrarily small ones of a local stability analysis are quite unlike those perturbations found in nature. Pimm modeled the perturbations as the deletion of single species from the community. A community is *species deletion stable* if, and only if, following the removal of a species from the community all of the remaining species are maintained at a new locally stable equilibrium (1982, 47). Pimm found that if only a basal species is deleted, the community's species deletion stability does not decrease with increasing interacting pairs of predators and prey. However, he did find that generally the number of interactions decreases the community's species deletion stability (1979, 355).

After this work by theoretical ecologists, Pimm recognized that one could articulate a variety of stability concepts (1984, 1991).¹⁹ Pimm, of course, was not the first to do so; C. S. Hollings and Gordon Orions had recognized this as well. Moreover, they all understood that with different stability concepts, one would have different hypotheses.

the complexity-stability question in ecological systems, his randomly constructed matrices must, of course, be representative of real ecosystems" (1978, 445). He claims that May's randomly constructed matrices *are* not representative and hence irrelevant to the central question. Lawlor argues that May has placed so few constraints on the biologically reasonable models, that a random search for a stable, biologically reasonable models would be a "transcomputational problem" (1978, 445). Thus, he tries to provide constraints so that a random sample will be representative of actual ecosystems and can overcome the computational problems. For a discussion of the idealizations in May's models, see Pimm (1984, 67-73)

¹⁸ For similar results with different models, see DeAngelis (1975), Gopin (1975), and Pimm (1979).

¹⁹ Greg Mikkelsen has argued that the stability concepts of May and Pimm create an "a priori bias" against the diversity-stability hypothesis (1999, 483). The "neighborhood stability" of a community concerns the probability that *all* the species must return to their pre-perturbation equilibrium abundances. Likewise, the species-deletion stability is the probability that *all* species avoid extinctions and hence persist after the perturbation. However, these criteria get increasingly strict as the number of species in a community grows. Hence, the stability concepts that May and Pimm employ turn an empirical issue into "an artifact of probability theory" (1999, 486). But, if a definition turns an empirical issue into a "generic a priori exercise," then we should reject such a definition. Mikkelsen argues that other stability concepts do not have this feature.

Nonetheless, Pimm distinguished between definitions of *complexity*, *stability*, and the *variables of interest*. The complexity of a community can be defined in terms of species richness, connectance, interaction strength, or evenness. Species richness is the number of species in a community. Connectance is the number of interspecific interactions divided by those possible. Interaction strength is the mean magnitude of interspecific interaction; i.e., the size of the effect of one species' density on the growth rate of another species. Species evenness is the variance of the species abundance distribution. The variables of interest are individual species abundances, species taxonomic composition, and trophic level abundance.

The "stability" of a community is thus characterized in one of the following ways (see 1984, 322)²⁰:

- A) *Stable*: a system is stable just in case all the variables return to their initial equilibrium values following a perturbation.
- B) *Resilience*: how fast the variables return to their equilibrium following a perturbation.
- C) *Persistence*: how long the value of a variable lasts before it changes to a new value.
- D) *Resistance*: the degree to which a variable is changed following a perturbation.
- E) *Variability*: the degree to which a variable varies over time.

Thus, the options for formulating a complexity-stability hypothesis have the three dimensions of complexity, stability, and variables of interest. There are four definitions of complexity, five of stability, and three variables of interest. This leads to a extremely large number of contending complexity-stability hypotheses.

There are several important methodological points to note from this discussion of the complexity-stability debate. First, whatever one thinks of the work of May and

²⁰ Orion's (1975) list of concepts consisted in trajectory stability, elasticity, inertia, and amplitude (1975, 141- 2) which is very similar to Pimm's.

Pimm—and many empirical ecologists have been skeptical—there has been a plethora of stability concepts that have arisen from the model building of the likes of May and Pimm among others. If this work had not been done, then the various hypothesis relating complexity and stability would not and could not have been imagined. As theoretical ecologist Hal Caswell (1988) argues,

None of these distinctions were, or could have been, drawn by Elton. Their importance became apparent only as the original verbal theory was studied using mathematical models. (1988, 35)

Thus, the models even if highly idealized and difficult to test, provided a conceptual framework for ecologist to study communities in the field and the lab. Otherwise, the concept, or better yet concepts, of ecological stability would have remained extremely vague.

Second, as these different hypotheses have been articulated with their associated stability concepts, ecologists have explored these hypotheses with experiments. Sharon Lawler (1993) studied protozoans in a laboratory “bottle experiment” to see if more complex food webs were more or less stable than simpler webs.²¹ Protist webs consisted in two, four, or eight species with each web replicated five times. The predator-prey pairs antecedently known to be stable were *Steina* and *Uronema* (S), *Blepharisma* and *Colpidium* (B), *Euplotes* and *Chilomonas* (E), and *Urostyla* and *Askenasia* (U). Thus, all the possible four species combinations of predator-prey pairs were (SB), (SE), (SU), (BE), (BU), (EU). Finally, the eight species combination is (SBEU). Only 1 of 40 populations (2.5%) went extinct in the two species-webs, whereas 26 out of 120 populations (21.7%) went extinct in the four-species webs, and 11 out of 40 populations

²¹ These microcosms are literally bottle experiments—each community existed in a 240 m glass jar of well water containing 100ml of Carolina Biological protozoan pellets.

(27.5%) went extinct in the eight species webs. Lawler drew the conclusion that more complex food webs produce more frequent extinctions in simple laboratory communities. This result is clearly in qualitative agreement with ‘May’s theorem’.

It is interesting to note that the work both theoretical and experimental that was suggested by his analyses of complexity and stability was exactly what he hoped would be accomplished through his models. He writes,

This work seeks to gain general ecological insights with the help of general mathematical models. That is to say, the models aim not at realism in detail, but rather at providing mathematical metaphors for broad classes of phenomena. Such models can be useful in suggesting interesting experiments or data collecting enterprises, or just in sharpening discussion (1973, v).

Models perform a variety of functions in theoretical ecology. They are used to explore possibilities, investigate complex systems, and provide conceptual frameworks. One of the functions that I have not described is in generating accurate predictions. In many cases, ecological models do provide accurate predictions. However, in evaluating the success and importance of models in ecology we must attend primarily to how they are used. That is, we must recognize the functions they are designed to perform by ecologists. Insofar as models accomplish those functions, we can count those models as successful. Models that are inaccurate can still lead to significant truths; it is just that the models themselves do not have to be true or accurate representations for some of the purposes to which they are put.

Simberloff’s worry

I now want to return to Daniel Simberloff’s worry expressed above since it is especially relevant to the pragmatic approach developed here.

Ecology is awash in all manner of untested (and often untestable) models, most claiming to be heuristic, many simple elaborations of earlier untested models. Entire journals are devoted to such work, and are as remote from biological reality as are faith-healers.

I take his concern to be the following: if models are to be of use—even as heuristics—they must ultimately answer to data. However, many models are built which have not been tested and they themselves are built from models that have not been tested either. Hence, these models are not being tested and thus are of little or no use.

Let us suppose that we have a family of related ecological models all deriving from some initial model. We start with a basic model from which all the others are generated and this model forms the basis of a structural framework, which other models descend from by virtue of having different assumptions along with some that are shared. The initial model might be our Lotka-Volterra predator-prey model and the other models might be our predator-prey model with a logistic term, or a predator-prey model with a logistic term and a predator satiation term, and so on. To devise a model that answers to empirical phenomena, we often must devise models tailored to specific systems and this often takes quite a bit of time. Our earliest models in the family will be more idealized and will be most difficult to test predictively. Thus, the aim by which they are judged will not be predictive accuracy and it will then be inappropriate to judge them against an aim they were never designed nor intended to fulfill. Hence, if Simberloff's criticism is that *all* models in such a family should be evaluated by their predictive accuracy, then this is extremely unreasonable. On the other hand, if his criticism is that *some* models in such a family should be tested predictively, then this is correct and consistent with what I have

claimed in this essay. In either case, Simberloff's criticism can be defused.²²

Nonetheless, one of the fundamental aims of science, and maybe the most fundamental, is empirical accuracy. Simberloff is exactly right—we do want models to “save the phenomena”. As Robert Brandon has argued, population biology is both “theory-rich” and “data-poor” but also “data-rich” and “theory-poor” (1993). In many cases, we do not have the right sort of theory for the data we possess and vice-versa. What this speaks to is not the bankruptcy of theory but rather that we do not have the proper interaction between theory, experiment, and data (Karieva 1993). As E. C. Pielou writes concerning models of limiting similarity,

They demonstrate, also, the difficulty of linking theoretical arguments to real-life situations. The existence of difficulties is not, of course, a deterrent; work should continue until they are overcome. (1974, 354)

Modelers and empiricists must be conversant with each other's work. To abandon theory is no solution. In fact, I would also suggest that model building is inescapable. Ecologists use mathematical models in order to develop general claims concerning various functional kinds even when those generalizations are not laws. Likewise, models, or concepts developed from them, can direct ecologists to crucial questions. Without our models, many questions might not have even been asked nor answered.

Lastly, I would suggest that conservation biology cannot be carried out without theoretical models. For example, one recent trend in applied ecology is population viability analysis (Soule 1985). Here ecologists use models in order to project the

²² Of course, Simberloff might claim that the proportion of tested models to the total number of models in a family is less than optimal. This claim would raise very perplexing issues. What is this “optimum”? How does one determine it?

expected time to extinction of various species with respect to specific periods of time and population sizes. PVAs require computer simulations based on simple population growth equations, Leslie projection matrices, and models of demographic and environmental stochasticity. Unfortunately, we simply lack the relevant data since these populations are so small and this induces massive sampling error. Moreover, if one experiments on an at risk population, then this can lead to its extinction. Hence, these analyses must be carried out with models even if they are not especially accurate. Thus, model building is an essential part of theoretical ecology, and even applied ecology.

Conclusion

The strategy of model building is important in the development of population and community ecology. Models are used for a variety of purposes such as exploring possibilities, investigating complex systems, providing conceptual frameworks, and generating accurate predictions. However, models must be evaluated according to their functional roles not against jobs that they are not designed to carry out. As Richard Levins writes,

Modelers always must keep in mind that the utility of their construct depends on the particular purpose for which it was built. There is no such thing as *the true model* of a system but only more or less adequate representations of the system. (1985, 8)

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