In Roughgarden et al

Chapter 5

Renewing the Dialogue between Theory and Experiments in Population Ecology

PETER KAREIVA

—

Theoretical population ecology has never been more vigorous. We have models for age-structured populations (Hastings 1986; Nisbet and Gurney 1986), stochastic environments (Chesson 1985), spatial heterogeneity (Levin 1978), and just about every type of species interaction imaginable (see, e.g., Edelstein-Keshet 1986; Addicott 1981; Pacala 1986). Not only is theory tackling the complexity and diversity of nature, but more and more models are being phrased in mechanistic terms (e.g., Tilman 1977, 1982). Although robust general predictions seem out of the question, models are generating numerous hypotheses and insights regarding particular classes of species interactions.

However, the current glories of theoretical population biology remain unknown to most ecologists. Experimental ecology and theoretical ecology are developing as almost separate fields and both pursuits suffer as a result. The main theme of this essay is that the future of theoretical ecology depends not on "better models," but on a constructive dialogue between theoreticians and empiricists. I will try to go beyond this platitude to point out specific avenues that will further the sort of dialogue I think is desirable. I begin with a brief historical tour, because the past provides numerous concrete examples of the rewards gained when mathematical models are intertwined with experiments.

THE BIRTH OF ECOLOGICAL THEORY SHIFTED THE EMPHASIS IN ECOLOGY FROM THE PHYSICAL ENVIRONMENT TO BIOTIC INTERACTIONS

Lotka, Volterra, Gause, Nicholson, and Bailey are men whose names are known to most ecologists. They were the founders of theoretical ecology and it is their

models that still appear in most introductory texts. Interestingly, of these five innovators, only Nicholson had much interest in natural populations or experience with them. Gause was a laboratory biologist, Bailey a physicist enlisted by Nicholson to help with mathematics, Volterra an applied mathematician, and Lotka a chemist. In spite of their different backgrounds, these early theorists shared the conviction that biology in general, and ecology in particular, would be more scientific if it could be made more mathematical. Whether, in fact, the mathematical approach did make ecology a "more scientific" discipline is perhaps debatable; but there is no doubt that the early theoretical treatments of species interactions profoundly influenced how ecologists studied the natural world.

Before 1930, ecology was an essentially descriptive compendium of correlations and anecdotes. Fluctuations in the numbers of plants and animals were usually explained in terms of changing physical factors, such as temperature, rainfall, or even sunspots (Kingsland 1985). Models of species interactions introduced a new way of explaining population dynamics—the models made it clear that biotic influences such as competition or predation could reliably cause population densities to change. Furthermore, the models identified predictable patterns of change. For instance, a tendency toward cycling was inextricably linked to predator-prey and host-parasitoid interactions. Interspecific competition was shown to lead to the exclusion of one species unless the interaction satisfied rather special requirements. There was even the hope that simple (yet defensible) assumptions about how an organism moved, fed, and grew could yield precise quantitative predictions of population trajectories (Nicholson and Bailey 1935).

Ecology had suddenly found a theory that was not only predictive but also quantitative, far-reaching, and testable. With hindsight, much of this theory may look either wrong or trivial. Yet, at the time of their conception, the first models of species interactions provided insights unanticipated by field ecologists (e.g., predator-prey cycles).

THE EARLY MODELS PROMPTED ZEALOUS COMPARISONS WITH FIELD OBSERVATIONS AND FIERCE EXPERIMENTAL SCRUTINY IN THE LABORATORY

A dialogue between theory and data was initiated soon after Lotka's (1925) and Volterra's (1931) contributions were published. Biologists did not need to understand the mathematical details of the models in order to appreciate their implications. For example, although its mathematics were a mystery to him, Elton realized that Volterra's model of oscillating predator-prey systems might help explain small-mammal population cycles (Kingsland 1985). Indeed, advocates and disciples of the new mathematical approach tended to find support for Lotka-

Volterra models throughout the natural world. Volterra and D'Ancona (1935) interpreted fluctuations in certain fish populations as verification of Volterra's predicted periodic cycles. Fluctuations in beetle populations that were attacked by a parasitic wasp were also cited as documentation of Volterra cycles (Chapman 1933). Of course, these examples always had alternative explanations and most ecologists remained skeptical of the models (Kingsland 1985). No one attempted to test any of the models experimentally in the field, but at the time field experiments of any kind were rare.

Although Lotka-Volterra and Nicholson-Bailey models were only impressionistically compared to field data, they were rigorously scrutinized in laboratory experiments (e.g., Gause 1934; Crombie 1946; Park 1948; Utida 1953, 1957). The usual approach was to pit one competitor against another, or a predator against its prey. If short-term observations (e.g., of instantaneous rates of population change) could be used to predict long-term population trajectories, then the models were thought to be supported. For practical purposes, these experiments invariably involved small organisms with short generation times, such as protozoans, mites, and insects. Because the organisms were usually cultured in small containers, these investigations have been labeled "bottle experiments." Although such experiments could not mimic the complexity of nature, they were the logical arena in which to first test models of species interactions. Only after Lotka-Volterra equations had proven their merits with *Paramecium* cultures (Gause 1934), did it make much sense to pursue the broader implications of these models.

Of course, the results of bottle experiments were not always in accord with theory. For example, contrary to the predictions of Volterra's predator-prey models, Gause (1934) found that predatory *Paramecium* and their prey (yeast) did not cycle with an amplitude determined by initial densities. In a separate set of experiments he also found that the consumption of *Paramecium* by carnivorous *Didinium* depended more on the predator's than on the prey's density, whereas Volterra's models implied that the consumption of prey depends equally on predator and prey density. Motivated by these experimental results, Gause, Smaragdova, and Witt (1936) altered Volterra's models to include a nonlinear functional response; these revised models produced dynamics more in accord with the experimental data. Lotka-Volterra models were also not always effective at predicting the outcome of interspecific competition in laboratory experiments. For instance, Park (1948) observed that under some circumstances it was impossible to determine which of two flour beetle species would win their competitive struggle. This clash of competition theory and data stimulated the development of stochastic models of interspecific competition (Leslie and Gower 1958). In general, dialogue between theory and experiment was frequent between 1930 and 1960. The two approaches were informing one another in an iterative fashion and, as a result, ecology made great advances.

POPULATION ECOLOGY LANGUISHED WHILE COMMUNITY ECOLOGY BOOMED DURING THE "MACARTHUR ERA"

The impact of Robert MacArthur on ecology was enormous. He made community ecology an exciting and theoretical subject, but in doing so attention was diverted away from population ecology. Because MacArthur's approach often began with the assumption that populations were at a steady state, the study of population dynamics was pushed into the background. MacArthur tended also to shun bottle experiments (MacArthur 1972; Schoener 1972), which had played such an important role in the initial testing and elaboration of Lotka-Volterra and Nicholson-Bailey equations. MacArthur's focus on communities, deemphasis of dynamics in favor of statics, and devaluation of bottle experiments catalyzed major changes in theoretical ecology. An unfortunate side effect was that the link between models and experiments was weakened. This happened because the models that dominated during the MacArthur era (i.e., niche overlap community models) were not subjected to experimental testing (Simberloff 1983). Bottle experiments could have been used, but as already mentioned, they had fallen from favor. The ecologists who were pioneering the use of field experiments (e.g., Connell 1961; Paine 1966) happened not to be in the business of testing niche-overlap models. Temporarily at least, the modeling approach and experimental approach appeared to fall into two distinct camps. The legacy of this peculiar history is that numerous ecologists mistakenly believe that mathematical theory in ecology is divorced from the real world and from experimental scrutiny. If this divorce has occurred, there is no reason that a reconciliation cannot be accomplished.

GENERAL THEORIES ARE REPLACED BY MORE RESTRICTIVE MODELS OF SPECIAL CASES

I suspect very few contemporary mathematical ecologists hold out much hope for a general theory of species interactions. Gone also is the idea that models can be conveniently "tested" by simply reporting a coincidence between observed patterns in nature and a model's predictions. Theoretical population ecology is now concerned largely with models that are tailored to particular systems, or that examine particular complications. Thus, instead of Lotka-Volterra equations, we now have models of plant-insect interactions (Edelstein-Keshet 1986), of competition among annual plants (Pacala 1986), of viruses attacking insects (Anderson and May 1980), and so forth. Also, instead of examining interactions in general, theoreticians tend now to analyze how each additional complicating factor influ-

ences the interaction. For example, in the area of predator-prey theory, there have been recent theoretical studies of the effects of age structure on predator-prey systems (e.g., Hastings 1986); the role of variability in predator-prey dynamics (e.g., Chesson 1978); and the importance of spatial heterogeneity in predator-prey interactions (Hastings 1978). The price of this increased sophistication has been a loss of generality (as was anticipated by Levins 1968). Nonetheless, recent theoretical explorations have yielded major new insights about species interactions. Some modern theoretical results of which all ecologists should be aware include the following:

1. *Simple difference equations yield complex dynamics.* Recursion models that project populations at time *t* forward to time *t* + 1 are capable of generating periodic cycles and chaotic fluctuations under the most minimal assumptions. The key requirement is that the function that transforms a current population into the next time period's population has a "hump" (i.e., it is low at low densities, rises to a peak at some intermediate density, and then falls off at extremely high densities). This assumption is clearly met by numerous fish and insect populations (Ricker 1954). The importance of this result is that many of the seemingly complex fluctuations observed in natural populations may be an inescapable feature of discrete reproductive episodes combined with density-dependent recruitment (May and Oster 1976).

2. *The spatial dimension of environments can facilitate the coexistence of species.* When Huffaker (1958) manipulated the spatial complexity of a simple laboratory environment, he observed dramatic changes in the dynamics of an interaction between predator and prey mites. This single experiment inspired scores of mathematical ecologists to examine the influence of the spatial environment on species interactions. An important finding has been that when the environment is broken into patches, even if all patches are the same, species can coexist that could never coexist were they to interact in one patch alone. Coexistence in such patchy environments depends on the proper ratios of dispersal abilities among the interacting species and on an average level of dispersal that is intermediate (Levin 1974). If there is too much movement among patches, the system behaves as one patch; if there is too little movement, populations will disappear from patches more rapidly than they can be reestablished in empty patches.

3. *Species interactions coupled with movement can generate spatial patterning in the densities of organisms.* Spatial patterns, by which I mean regular inhomogeneities in population densities, are found in a variety of ecological systems (Kareiva and Odell 1987; Levin 1978). Reaction-diffusion models show that such patterns can arise as a result of the interaction and redistribution of species *without any underlying environmental heterogeneity.* Plausible models of predator-prey interactions with dispersal (Levin and Segel 1976) and of competitive in-

teractions with dispersal (provided at least three species are involved; Mimura 1984) can lead to predictable spatial patterns. These spatial patterns, which are sometimes called "diffusive instabilities" (Levin and Segel 1985), occur when inhibiting factors (e.g., predators) spread significantly faster in space than do activating factors (e.g., prey).

4. *Stochastic environments can convert competitive exclusion into competitive coexistence.* Whereas it was once thought that environmental variability acted to eliminate species (e.g., Goh 1975, 1976; Leigh 1975), it has now been shown that environmental variability may act to preserve species diversity. In particular, competing species that cannot coexist in a constant environment may be able to coexist in the presence of environmental variation (Chesson 1985). Recent models by Chesson (1988) allow us to predict under which circumstances variability will preserve species and under which circumstances variability will eliminate species.

5. *The potential role of diseases in population dynamics has been clearly demonstrated.* Diseases were neglected in early considerations of population dynamics. During the last decade, however, a series of papers by Anderson and May (e.g., 1979a, 1979b, 1980) have shown that diseases can stably maintain their host populations at depressed densities or can generate periodic cycles of host abundance. Most importantly, the levels of virulence required for these effects are within the range that has been measured for many viral and bacterial pathogens.

6. *Age structure can have both stabilizing and destabilizing effects on species interactions and population dynamics.* Although age-structure effects have long been known to influence quantitative aspects of population dynamics, their influence on qualitative behavior has only recently been delineated (Nisbet and Gurney 1986). The effects of age structure are complex, but appear to follow two routes: (1) age structure may be destabilizing because it introduces time delays into the negative feedbacks that dampen population growth, or (b) age structure may be stabilizing because it distributes perturbations over several different cohorts in a population (Hastings 1984; Levin and Goodyear 1980). General predictions about when to expect stabilizing effects and when to expect destabilizing effects have not, as yet, been possible.

7. *The extent of clumping among individuals can determine the outcome of species interaction.* Most plants and animals live clustered or "aggregated" together with other individuals of the same species (Taylor 1971). The degree of aggregation can have profound consequences for host-parasite (Anderson and May 1986), predator-prey (Hassell and May 1974), and competitive interactions (Atkinson and Shorrocks 1984; Ives and May 1985). Since aggregation is a product of individual movements, theories that relate aggregation to population dynamics hold the promise of connecting population ecology to behavioral ecology (Hassell and May 1985).

In addition to the above general results, theoreticians have also made progress modeling particular systems. For example, detail-rich models have been able to describe population interactions in rocky intertidal communities (Paine and Levin 1981; Roughgarden, Iwasa, and Baxter 1985), among ladybird beetles and aphids (Kareiva and Odell 1987), among forest defoliators and their host trees (Ludwig, Jones, and Holling 1978), and so forth. Although these species-specific models cannot be easily transferred to other assemblages, they do provide general lessons about how to build a quantitative understanding of population interactions. In all instances the models succeed not because they faithfully reproduce the complexity of nature, but because they identify a biological feature that is key to the process being studied. For instance, Paine and Levin (1981) identify the magnitude and frequency of disturbance as the critical variable influencing competition for space among sessile intertidal organisms; Roughgarden, Iwasa, and Baxter (1985) emphasize larval settlement as a determinant of barnacle population dynamics; Kareiva and Odell (1987) build a predator-prey model upon the critical assumption that predators alter their movement behavior after feeding; Ludwig, Jones, and Holling (1978) explain budworm cycles in terms of inexorably slow changes in forest quality coupled with potentially rapid changes in budworm populations. All of these success stories entailed extensive biological understanding before the appropriate mathematical simplifications could be crystallized.

THE LIST OF CRITICAL EXPERIMENTS THAT NEED DOING IN POPULATION ECOLOGY IS LONG

Theorists have been so busy, and empiricists have been so inattentive to theory, that an enormous backlog of experimental work has accumulated. An obvious agenda would be to start experimentally testing the theoretical results listed in the preceding section. This is not going to be easily accomplished because many theoretically important factors are difficult to manipulate experimentally. For instance, there is no convenient way of altering the age structure of interacting populations. Another problem is that as models have increased in sophistication, fewer and fewer ecologists are inclined to follow their arguments closely. In addition, today's ecologist faces an overwhelming selection of models from which to choose (whereas in the 1940s and 1950s there was only a handful to consider). Even ecologists who are sympathetic and supportive of mathematical theories cannot help but be bewildered by the current state of mathematical ecology. However, rather than be discouraged by the explosion of mathematical modeling, we should be grateful to theory for identifying such a long list of critical experiments:

1. *We need more bottle experiments.* Ecologists gave up bottle experiments too soon. For example, such experiments would be particularly valuable in studying

the chaotic fluctuations associated with nonlinear difference equations. These intrinsically driven cycles are best studied in a laboratory environment, where environmental fluctuations can be eliminated. Although the mathematical significance of chaos is unarguable, there is disagreement as to whether organisms possess the life-history traits required for generating chaos (Prout and McChesney 1985). Not only would bottle experiments reveal if the recruitment functions of real organisms made them candidates for chaotic dynamics, but they may also uncover additional routes to chaos. For instance, in a rare recent series of "bottle experiments," Prout and McChesney (1985) found that a dependence of fruit-fly fertility on egg density introduced a time delay that enhanced the likelihood of chaos. If this delay is ignored, as it has been by many previous researchers, one gets the mistaken impression of simple stable dynamics. Another promising avenue for bottle experiments is the study of host-pathogen coevolution using bacteria-phage interactions (Lenski and Levin 1985). Because of the short generation times and measurable mutation rates of phages and bacteria, it is actually possible to test models of coevolution.

2. *Measure and manipulate dispersal.* The role of dispersal in species interactions is now well established theoretically. The obvious experiment is to manipulate dispersal rates of organisms and observe subsequent population dynamics (Kareiva 1987). If theory is correct in attaching so much importance to dispersal, one should be able fundamentally to alter the outcome of competitive or predator-prey interactions by adjusting rates of movement. Such adjustments are practical for many plant-insect systems (e.g., Kareiva 1984; Bergelson and Kareiva 1987).

3. *Follow populations of competing plant species through several generations.* When competition models were first being examined for animals, multigeneration experiments (Crombie 1945; Gause 1934) helped in the evaluation and refinement of the models. Competition models are just now being formulated for plants (Pacala 1986, 1987), but there are no experimental data concerning population trajectories of competing plants. Instead, experiments on plant competition have always been terminated after a single generation, which is a sensible practice for an agronomist concerned with yields, but is inadequate for a botanist concerned with modeling the dynamics of competition.

4. *Huffaker's experiments warrant repeating and elaboration.* Huffaker's classic experiments with mites and oranges provoked two decades of spatial heterogeneity modeling. These later models now provide a broad menu of predictions concerning the influence of patchiness on species interactions (e.g., Hastings 1978; Caswell 1978; Crowley 1979; Hilborn 1975). It would be useful to return to the sort of laboratory experiments that stimulated these models and manipulate the patchiness of microcosms. In some cases this approach could also be applied to interactions in natural communities (e.g., Kareiva 1987).

5. *Manipulate the degree of aggregation.* Aggregation figures prominently as a stabilizing feature in several predator-prey (Hassell and May 1974; Hassell

1978) and competition (Ives and May 1985) models. In theory at least, the tendency of organisms to cluster together could be a primary factor permitting coexistence of species. This idea has been evaluated to date only by showing that observations of unmanipulated field systems are either consistent or inconsistent with phenomenological models of aggregation and interaction. A direct test would be to manipulate the degree of aggregation in selected species and look for predicted changes in predator-prey or competitive contests. Such an approach would be practical with insects, where eggs or early instar individuals can be arranged experimentally in a variety of dispersions.

6. *Test the influence of environmental variability on competing species.* Chesson's models (1985, 1986, 1988) concerning variability and competition are widely discussed and among the most interesting theoretical advances in modern ecology. Yet these models have never been tested. Since Chesson (1988) is able to relate the influence of variability on coexistence to its influence on recruitment rates, one could select species whose recruitment functions respond differently to variability and then ask whether the competitive interactions respond to variability as predicted by theory. Alternatively, one could select a particular interaction and manipulate the magnitude of variability. These will be challenging experiments to perform, but the importance of the theory makes them worth the investment.

7. *Manipulate habitat geometry.* Several models indicate that the size, shape, and spatial arrangement of habitat patches should influence an organism's population density (Okubo 1980), its likelihood of extinction or establishment (Lefkovitch and Fahrig 1985; Quinn and Hastings 1988), and its interactions with other species (Okubo 1980). At the same time, it is widely recognized that one of mankind's major impacts is to fragment and alter the geometry of habitats. The combination of ready-made theory and a practical need for information on the effects of habitat shape or fragmentation should be a strong impetus for experimental manipulations of habitat geometry. Some of the manipulations suggested by theory are (a) manipulate the size of habitat patches and determine whether there is some minimum size below which populations go extinct (Okubo 1980) or explode (Ludwig, Aronson, and Weinberger 1979); (b) manipulate the ratio of a patch's perimeter to its area and look for changes in the density of residents (Kareiva 1984); (c) manipulate the spatial arrangement of a fixed number of patches (Lefkovitch and Fahrig 1985); and so forth. Unfortunately, unless direct observations are made of movements into, out of, or among habitat patches, there will be no way of ascribing the results of such experiments to particular mechanisms. Studies of habitat geometry are becoming fashionable under the rubric of "landscape ecology," but in the absence of guiding models, key data are neglected and the value of the experiments is diminished.

8. *Build population models out of microscale observations of individual behavior.* It should be possible to predict population dynamics from observations of indi-

vidual feeding behavior and of birth and death schedules. This approach does not yield general models but it does allow one to determine how well a particular system is understood. The experiments that underlie this research stragegy can be laborious, but they sometimes lead one to discover important consequences of "minor" changes in behavior (see Hassell and May 1974 or Kareiva and Odell 1987 for examples). I think the key to successful behavior-based models is parsimony in the number of parameters included in the models and cleverness about quantitatively summarizing complex behaviors. However, other theoreticians have argued that we need to take advantage of new computer software (e.g., artificial intelligence programs) and build increasingly complicated models if we are to meld behavioral ecology and population ecology (see, for example, Franklin and Taylor 1988).

9. *Test three-trophic-level models.* Somewhere between classical population ecology and community ecology lie three-trophic-level models. These models are amenable to the same sorts of experiments that have proven useful in studying pairwise competitive interactions and predator-prey interactions (see, e.g., Morin 1983). However, although three-trophic-level interactions are much discussed by ecologists (e.g., Price et al. 1980), they have yet to be attacked by a joint modeling and experimental approach.

10. *Explore the population-level consequences of phenotypic and genetic variability.* Organisms in any population usually differ markedly because of phenotypic plasticity or genetic variability. Regardless of its causes, ecologists tend to ignore variability among organisms, even though they have no assurances that such a simplification is justified. More attention (theoretical and experimental) needs to be given to the consequences of variability for population interactions. Here, I think the mathematical investigations will be more difficult than the experiments. It is a simple matter to manipulate the magnitude of variation within interacting populations (e.g., Antonovics and Ellstrand 1984), but it is not a simple matter to include variability among individuals in equations of population change. Thus, for their own sake as well as to direct theory, we need experimental studies in which the effects of variability on predator-prey, plant-herbivore, and competitive interactions are examined. In addition to its basic importance, the issue of variability also has an applied dimension. It is well known that genetic variability is being eroded in many species. While evolutionary biologists have been quick to point out the evolutionary consequences of this reduced variability, ecologists have said little about the implication of diminished variability for population dynamics.

I am sure there are many other critical experiments than those in the above list. In general, the influence of heterogeneity, variability, and movement demand the most experimental attention. These are the influences that have received the greatest and most original theoretical attention over the last few decades. It is time

to inspect this theory in the light of data. The most satisfying experiments will involve the clean manipulation of a single factor targeted by theory (e.g., movement rate or spatial variability) and then comparison of results to predictions. Another satisfying approach involves independently estimating model parameters and quantitatively predicting population dynamics in a novel situation (see, e.g., Kareiva and Odell 1987). Where manipulation or independent estimation of parameters is impossible, models can still be tested by asking whether they are sufficient to explain observed dynamics given plausible parameters (e.g., Ludwig, Jones, and Holling 1978).

Rather than wanting to test models, most field ecologists are interested in particular biological questions or systems. Even in these situations models can guide an experimental program in profitable ways. For example, William Murdoch and colleagues have been studying biocontrol systems for the last decade. Their central question has been: What factors contribute to the success of biological control programs (Murdoch, Chesson, and Chesson 1985)? Although there has never been a specific model proposed, each step of the inquiry has addressed the assumptions or predictions of general phenomenological models concerning host-parasitoid interactions. The result is that weaknesses in the theory have been exposed (e.g., in the treatment of aggregation) and alternative models developed. At the same time, the models, although imperfect, have informed Murdoch and colleagues as to which data to collect. The concrete results of this interaction between theory and experiment are considerable: (1) we know that aggregation of the sort required for effective biological control is either hard to detect or unimportant (Chesson and Murdoch 1986; Murdoch, Chesson, and Chesson 1985; Reeve and Murdoch 1985); (2) a stable biocontrol system has been found in which the existence of a refuge appears to be key to stability (Reeve and Murdoch 1986); (3) the attention of theorists is turning toward more mechanistic models of aggregation (Kareiva and Odell 1987). This progress did not require an explicit model to be tested, but simply that the experimentalist was well aware of the pertinent models.

WHY EMPIRICISTS NEED THEORIES

It is well known that empiricists are needed to occasionally constrain the imaginations of theorists. Less obvious is the need empiricists have for theory, especially since so often they seem to be quite productive without worrying about models. Several authors have eloquently described the contributions mathematical models make to experimental ecology (Levins 1968; Levin 1981; May 1981). These contributions include clarifying hypotheses and chains of argument, identifying key components in systems, suggesting critical experiments, and introducing new ideas. Models may also give an empiricist confidence in a

particular idea and the motivation to collect data that otherwise would have been ignored (see discussion of Dobzhansky and theoretical population genetics models in Mayr and Provine 1980). In addition, models are needed to determine whether specific processes can account for observed phenomena. For instance, if mark-recapture studies indicate that butterflies move on average 10 meters from their release point within one day, how far should the butterflies have moved after one week? Or at what rate should the range of these butterflies expand into a new habitat, assuming logistic population growth and only local movement? These questions can be addressed only by examining models.

Simultaneous consideration of spatial and temporal population dynamics provides another reason for models. Verbal reasoning simply does not work well when one is trying to determine the influences of both movement and local interactions. Counterintuitive results such as the "diffusive instabilities" mentioned previously cannot be understood without mathematics. It is hard even to present spatiotemporal data, much less interpret it, without some modeling framework.

Ecologists have also become concerned with processes operating at large spatial scales (i.e., landscapes) and over long time periods. Experiments in ecology typically collect data from a few square meters over a couple of field seasons (Kareiva and Andersen 1988). A central question is, to what extent does the understanding we obtain from our brief, small experiments extrapolate to large-scale phenomena? This question can be economically answered by using models to make the extrapolation, and then comparing predictions to observed processes. In general, the study of large-scale processes will increasingly demand models since experiments at large scales are prohibitively expensive or unreplicable. In these situations, one value of models is the guidance they can provide as to which experiments can provide the most information. When only a few experiments can be done, one cannot allow empiricism to proceed in an ad hoc fashion.

One final use of models is as a framework for data standardization. As it is currently practiced, ecology involves too little standardization. For instance, hundreds of mark-recapture studies have been performed with the goal of describing dispersal in insects. Yet the data from these studies have been reported in such haphazard and idiosyncratic ways that it is impossible to synthesize the results. A model might dictate a way of reporting such data; for example, numerous different movement models indicate that a diffusion coefficient (in terms of distance^2/time) would be a useful parameter to calculate from mark-release experiments (Okubo 1980). If theoreticians could convince researchers doing mark-release experiments to report diffusion coefficients, the study of dispersal would be greatly facilitated. It does not matter that diffusion models will not describe the movement of most organisms—the point is they identify a key parameter to measure. The functional response is a good example of models promoting useful data standardization. Because of Holling's (1965) and Hassell's

(1978) models, most experimentalists who study predator-prey interactions report a functional response; often they even do so according to standard equations. As a result of this practice, the effectiveness of different predators, studied by different researchers, can usually be compared (e.g., Lentern 1986; Olszak (1986). Naturalists often make the point that each species is unique and thus general models are probably impossible; but precisely because each species is different, we need to report data in some consistent fashion that readily allows comparisons. Models can indicate which standardizations will be most useful.

Models are more necessary for experimental ecology now than ever before, because ecology in general has become more sophisticated. The "easy questions," which yield to straightforward manipulations such as competitor removals or predator removals, have mostly been answered. Attention has now turned to processes that can produce cour ·erintuitive results. Spatial patterning in homogeneous environments, coexistence due to stochastic variation, and complex dynamics from recursion equations are all examples of phenomena that cannot be understood by intuition and verbal reasoning. They are also phenomena likely to play a major role in natural populations. Experimentalists are interested in interactions between competition and predation, rather than just predation or competition alone. The effect of such interactions is a quantitative question, again a question best addressed with the aid of models. Environmental problems demand quantitative answers from ecologists, not just platitudes about diversity and productivity, or about stability. Experimentalists have done a good job of documenting the sorts of effects species have on one another, but it is now time for models to predict the magnitude of these effects given various initial conditions.

HOW SHOULD THEORETICIANS BE INVESTING THEIR ENERGIES?

I often wonder if theoreticians realize the extent to which their work is ignored by field ecologists. It would be educational for all involved if each theoretician tried convincing at least one empiricist to test some favorite model. Not only might useful experiments get performed, but models would be improved through the process. The current standard for linking models to nature seems to be phrases of the form, "this model could apply to _____, which shares the features _____," or "this model is a metaphor for _____," etc. Such phrases are necessary and informative, but are not enough to stir the typical empiricist to action. Of course many models are not intended to make testable predictions, but are only indications of what might be. The messages these metaphorical models carry for field ecologists could nonetheless be made more transparent.

There are, however, more than communication problems to be overcome before theory becomes better integrated into ecology. Theoreticians need to put

greater effort into devising mechanistic models that include concrete, directly measurable parameters. Because they are often less general and more resistant to elegant analysis, such mechanistic models are less interesting to a theoretician. The theoretician's reward for developing special-case mechanistic models will be the attention of biologists. A good example is Tilman's recent model of resource competition among plants (Tilman 1982). Although many botanists disagree with Tilman's ideas, his model is extensively discussed and evaluated because it is mechanistic, and it suggests straightforward experiments (i.e., manipulating nutrient ratios).

Theoreticians also need to provide guides to the diversity of models now available. To some extent this will require original theoretical work. For example, virtually all populations are age-structured and live in heterogeneous environments; experimentalists need to know under what circumstances age structure is likely to be of overriding importance, and under what circumstances spatial heterogeneity is likely to have the greatest impact. To answer these questions alternative complications should be simultaneously analyzed in models, with the goal of identifying where in the parameter space different influences are most dramatic. Here, ratios of parameters can be especially useful—for instance, the ratio of a predator's dispersal rate to its prey's dispersal rate determines whether pattern formation is expected (Okubo 1980). The fact that ecological theory is pluralistic will not be a weakness if some form of "dichotomous key" to theory can be devised.

Studies in which models are applied to simulated noisy data have begun to appear in the literature (Hassell 1985; Ludwig and Walters 1985). These will be extremely useful both to theoreticians and to empiricists. Theoreticians can learn what level of model complexity is commensurate with the quality of data available. In some cases, estimation errors override the advantages of using "more realistic" comprehensive models (Ludwig and Walters 1985). Empiricists might learn that when a certain model holds, standard practices of collecting data gloss over key features of the dynamics. For example, Hassell (1985) found that k-factor analysis (which is supposed to quantify regulating factors) often fails to unmask population regulation in data sets contaminated by stochastic variation. Hassell is able to use this analysis to recommend alternative approaches to collecting data on host-parasite interactions.

In addition to the above general platitudes, certain specific problems in population ecology deserve more theoretical attention. It would be useful to build models of population dynamics at the landscape level from an understanding of local dynamics plus long-range transport. The framework for such models is well established (e.g., Levin 1978), but has never been applied to a large-scale system. Theoretical studies of species interactions that include dispersal need to examine the effects of taxis, aggregation, and other forms of transport that are more complex than simple diffusion. Models of plant-herbivore interactions have not yet dealt with the rich variety of plant

responses to herbivory (e.g., induced defenses, compensatory regrowth, etc.). The-
oretical description of plant population dynamics and plant competition pose some of
the greatest problems (Schaeffer and Leigh 1975). Existing models tend to be built
from curve-fitting routines rather than any underlying mechanism. To deal with the
spatial dimension, potentially undesirable assumptions about the dispersion of seeds
are often made. Frequency dependence, which several recent experiments suggest
may play a major role in plant competition (Antonovics and Kareiva 1988), is not
adequately treated in current models. Finally, important work also needs to be done
with basic models of predator-prey interactions. In particular, the significance of
differing foraging behaviors for population dynamics has not been adequately ex-
plored (Hassell and May 1985). While it is clear that animals forage in predictable
ways, theoreticians have at best only phenomenologically described the population-
level consequences of assorted foraging behaviors (the exception is Hassell and May
1974). It would be especially interesting to learn whether behavior that approximates
optimal foraging has any tendency to stabilize or destabilize predator-prey inter-
actions.

My recommendations in this area have been concerned largely with style and
communication, because I think theoreticians are doing an excellent job of ad-
dressing the important questions in ecology. Getting the models noticed and
tested by field biologists has been the weak link.

THE ROAD TO RENEWED DIALOGUE BETWEEN
THEORETICAL AND EXPERIMENTAL ECOLOGY IS
DANGEROUS

Because there are so many ways for empiricists and theoreticians to misunder-
stand one another, dialogue between their two approaches can be treacherous.
Although I have made a strong plea for more testing of models, I worry that this
appeal might be misconstrued into a demand that theoreticians conduct experi-
ments. That would be a waste of talent and would probably produce some
absolutely disastrous experiments. Empiricists need to realize that models and
theories go through a development process from abstract to specific—it would be
folly to demand that models be immediately couched in testable form. It is also
folly to demand that models faithfully adhere to reality (although they should
touch it in some tangible way); one of the virtues of theory is that the imagination
is freed from details so that new connections are revealed.

On the other hand, I also worry that my plea for improved communication on
the part of theorists might be misunderstood. There is always the danger that
theoreticians will be overzealous about "selling their models" and thereby mis-
lead empiricists. To avoid this, theoreticians need to be ever skeptical of their own
models and restrained in the claims they make for theory. Perhaps if empiricists

were more motivated to understand models, they would not need hyperbole to
prick their interest.

Many ecologists are completely ignorant of mathematical ecology. This igno-
rance is initially tolerated in undergraduate ecology courses, in which mathe-
matical models are usually avoided or discussed in a defensive manner. Graduate
programs further nurture this ignorance by allowing candidates to receive Ph.D.s
in ecology while knowing so little theory. The generally poor training in mathe-
matical ecology that most ecologists receive is inexcusable. There is no escaping
the fact that ecology is largely a science of births, deaths, numbers, derivatives, and
fluxes. But ecologists have been timid about insisting on mathematical literacy.
Progress in ecology will be slow as long as experimentalists are handicapped by a
fear or ignorance of basic mathematical reasoning.

A MILITANT SUMMARY

In summary, population ecology is rich with theory. Where theories have been
combined with experimental research, substantial advances have been made (e.g.,
Hassell and May 1974; Reeve and Murdoch 1986; Anderson and May 1979a,b;
Paine and Levin 1981; Lenski and Levin 1985). But the sad truth is that ecological
theory exists largely in a world of its own, unnoticed by mainstream ecology. If
ecology is ever to become more than a compendium of analysis of variance tables,
there must be a strong dialogue between theoreticians and empiricists. Militant
and immediate action is needed along two fronts: (1) theoreticians must become
more effective at making their models accessible and testable, and they must
produce some agreed-upon guidelines to help the empiricist through the maze of
models; and (2) empiricists must become more educated in the application of
mathematical reasoning to ecological questions. Past mistakes and the fact that no
grand unified theory is on the horizon should not detract from the contributions
models are likely to make to ecology.

ACKNOWLEDGMENTS

REFERENCES

Addicott, J. F. 1981. Stability properties of two-species models of mutualism: Simulation studies. *Oecologia* 49:42–49.

Anderson, R., and R. May. 1979a. Population biology of infectious diseases, I. *Nature* 280:361–67.

Anderson, R., and R. May. 1979b. Population biology of infectious diseases, II. *Nature* 280:455–61.

Anderson, R., and R. May. 1980. Infectious diseases and population cycles of forest insects. *Science* 210:658–61.

Anderson, R., and R. May. 1986. Helminth infections of humans: Mathematical models, population dynamics and control. *Adv. Parasitol.* 24:1–101.

Antonovics, J., and N. Ellstrand. 1984. Experimental studies of the evolutionary significance of sexual reproduction. I. A test of the frequency-dependent selection hypothesis. *Evolution* 38:103–15.

Antonovics, J., and P. Kareiva. 1988. Frequency-dependent selection and competition: Empirical approaches. *Proc. Roy. Soc. Lond. (B).* In press.

Atkinson, W. D., and B. Shorrocks. 1984. Aggregation of larval Diptera over discrete and ephemeral breeding sites: The implications for coexistence. *Amer. Natur.* 124:336–51.

Bergelson, J., and P. Kareiva. 1987. Barriers to movement and the response of herbivores to alternative cropping patterns. *Oecologia* 71:457–60.

Caswell, H. 1978. Predator mediated coexistence: A nonequilibrium model. *Amer. Natur.* 112:127–54.

Chapman, R. 1933. The causes of fluctuations of populations of insects. *Proc. Haw. Ent. Soc.* 8:279–92.

Chesson, P. 1978. Predator-prey theory and variability. *Ann. Rev. Ecol. Syst.* 9:323–47.

Chesson, P. 1985. Coexistence of competitors in spatially and temporally varying environments: A look at the combined effects of different sorts of variability. *Theor. Pop. Biol.* 28:263–87.

Chesson, P. 1986. Environmental variation and the coexistence of species. In J. Diamond and T. Case, eds., *Community Ecology,* pp. 240–56. Harper and Row, New York.

Chesson, P. 1988. A general model of the role of environmental variability in communities of competing species. In A. Hastings, ed., *Community Ecology,* pp. 68–83. Springer Verlag, New York.

Chesson, P., and W. Murdoch. 1986. Aggregation of risk: Relationships among host-parasitoid models. *Amer. Natur.* 127:696–715.

Connell, J. 1961. Effects of competition, predation by *Thais lapillus,* and other factors on natural populations of the barnacle *Balanus balanoides. Ecol. Monogr.* 31:61–104.

Crombie, A. 1945. On competition between different species of graminivorous insects. *Proc. Roy. Soc. Lond. (B)* 132:362–95.

Crombie, A. 1946. Further experiments on competition. *Proc. Roy. Soc. Lond. (B)* 133:76–109.

Crowley, P. 1979. Predator-mediated coexistence: On equilibrium interpretation. *J. Theor. Biol.* 80:129–44.

Edelstein-Keshet, L. 1986. Mathematical theory for plant-herbivore systems. *J. Math. Biol.* 24:25–58.

Elton, C. 1935. *Animal Ecology,* 2d ed. Macmillan, New York.

Franklin, R., and R. Taylor. 1988. Artificial intelligence simulation modeling for behavioral ecology. *Ecol. Model.* In press.

Gause, G. F. 1934. *The Struggle for Existence.* Williams & Wilkins, Baltimore.

Gause, G. F., N. P. Smaragdova, and A. A. Witt. 1936. Further studies of interaction between predators and prey. *J. Anim. Ecol.* 5:1–18.

Goh, B. 1975. Stability, vulnerability and persistence of complex ecosystems. *Ecol. Model.* 1:105–16.

Goh, B. 1976. Nonvulnerability of ecosystems in unpredictable environments. *Theor. Pop. Biol* 10:83–95.

Hassell, M. 1978. *The Dynamics of Arthropod Predator-Prey Systems.* Princeton University Press, Princeton, N.J.

Hassell, M. 1985. Insect natural enemies as regulating factors. *J. Animal Ecol.* 54:323–34.

Hassell, M., and R. May. 1974. Aggregation in predators and insect parasites and its effects on stability. *J. Anim. Ecol.* 43:567–94.

Hassell, M., and R. May. 1985. From individual behaviour to population dynamics. In R. Sibly and R. Smith, eds., *Behavioral Ecology,* pp. 3–32. Blackwell, Oxford.

Hastings, A. 1978. Spatial heterogeneity and the stability of predator-prey systems: Predator-mediated coexistence. *Theor. Pop. Biol.* 14:380–95.

Hastings, A. 1984. Simple models for age-dependent predation. *Lect. Notes in Bio-Math.* 54:114–21.

Hastings, A. 1986. Interacting age-structure populations. In G. Hallam and S. Levin, eds., *Mathematical Ecology,* pp. 287–94. Springer-Verlag, New York.

Hilborn, R. 1975. The effect of spatial heterogeneity on the persistence of predator-prey interactions. *Theor. Pop. Biol.* 8:346–55.

Holling, C. S. 1965. The functional response of predators to prey and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.* 45:1–60.

Huffaker, C. 1958. Experimental studies on predation: Dispersion factors and predator-prey oscillations. *Hilgardia* 27:343–83.

Hutchinson, G. E. 1978. *An Introduction to Population Ecology.* Yale University Press, New Haven.

Ives, A. R., and R. May. 1985. Competition within and between species in a patchy environment: Relations between microscopic and macroscopic models. *J. Theor. Biol.* 115:65–92.

Kareiva, P. 1984. Predator-prey dynamics in spatially-structured populations: Manipulating dispersal in a coccinellid-aphid interaction. *Lect. Notes in BioMath.* 54:368–89.

Kareiva, P. 1987. Habitat fragmentation and the stability of predator-prey interactions. *Nature* 321:388–91.

Kareiva, P., and M. Andersen. 1988. Spatial aspects of species interactions: The wedding of models and experiments. In A. Hastings, ed., *Community Ecology,* pp. 38–54. Springer Verlag, New York.

Kareiva, P., and G. Odell. 1987. Swarms of predators exhibit "preytaxis" if individual predators use area restricted search. *Amer. Natur.* 130:233–70.

Kingsland, S. 1985. *Modeling Nature.* University of Chicago Press, Chicago.

Lefkovitch, L., and L. Fahrig. 1985. Spatial characteristics of habitat patches and population survival. *Ecol. Model.* 30:297–308.

Leigh, E. G. 1975. Population fluctuations, community stability and environmental variability. In M. Cody and J. Diamond, eds., *Ecology and Evolution of Communities,* pp. 51–73. Harvard University Press, Cambridge, Mass.

Lenski, R., and B. Levin. 1985. Constraints on the coevolution of bacteria and virulent phage: A model, some experiments, and predictions for natural communities. *Amer. Natur.* 125:585–602.

Lentern, J. 1986. Evaluation of effectiveness and utilization. In Hodek, ed., *Ecology of Aphidophaga,* pp. 505–10. Dr. W. Junk, Prague.

Leslie, P. H., and J. Gower. 1958. The properties of a stochastic model for two competing species. *Biometrika* 45:316–30.

Levin, S. 1974. Dispersion and population interactions. *Amer. Natur.* 108:207–28.

Levin, S. 1978. Population models and community structure in heterogeneous environments. In S. Levin, ed., *Studies in Mathematical Biology,* part 2, pp. 439–76. American Mathematical Association, Washington, D.C.

Levin, S. 1981. The role of theoretical ecology in the description and understanding of populations in heterogeneous environments. *Amer. Zool.* 21:865–75.

Levin, S., and C. Goodyear. 1980. Analysis of an age-structured fishery model. *J. Math. Biol.* 9:245–74.

Levin, S., and L. Segel. 1976. Hypothesis for the origin of plankton patchiness. *Nature* 259:659.

Levin, S., and L. Segel. 1985. Pattern generation in space and aspect. *SIAM Review* 27:45–67.

Levins, R. 1968. *Evolution in Changing Environments.* Princeton University Press, Princeton, N.J.

Lotka, A. 1925. *Elements of Physical Biology.* Williams & Wilkins, Baltimore. (Reprinted 1956 by Dover Press, New York.)

Ludwig, D., D. Aronson, and H. Weinberger. 1979. Spatial patterning of the spruce budworm. *J. Math. Biol.* 8:217–58.

Ludwig, D., and C. Walters. 1985. Are age-structured models appropriate for catch-effort data? *Can. J. Fish. Aquat. Sci.* 42:1066–72.

Ludwig, D., D. Jones, and C. S. Holling. 1978. Qualitative analysis of insect outbreak systems: The spruce budworm and the forest. *J. Anim. Ecol.* 47:315–32.

MacArthur, R. 1972. *Geographical Ecology.* Harper and Row, New York.

May, R. 1981. The role of theory in ecology. *Amer. Zool.* 21:903–10.

May, R., and G. Oster. 1976. Bifurcations and dynamic complexity in simple ecological models. *Amer. Natur.* 110:573–99.

Mayr, E., and W. Provine. 1980. *The Evolutionary Synthesis.* Harvard University Press, Cambridge, Mass.

Mimura, M. 1984. Spatial distribution of competing species. *Lect. Notes BioMath.* 54:492–501.

Morin, P. 1983. Predation, competition, and the composition of larval anuran guilds. *Ecol. Monogr.* 53:119–38.

Murdoch, W., Chesson, J., and P. Chesson. 1985. Biological control in theory and practice. *Amer. Natur.* 125:344–66.

Nicholson, A., and V. Bailey. 1935. The balance of animal populations. *Proc. Zool. Soc. Lond.* 3:551–98.

Nisbet, R., and W. Gurney. 1986. The formulation of age-structure models. In G. Hallam and S. Levin, eds., *Mathematical Ecology,* pp. 95–116. Springer-Verlag, New York.

Okubo, A. 1980. *Diffusion and Ecological Problems: Mathematical Models.* Springer-Verlag, New York.

Olszack, R. 1986. The effectiveness of three species of coccinellid adults in controlling small colonies of the green apple aphid. In Hodek, ed., *Ecology of Aphidophaga,* pp. 381–84. Dr. W. Junk, Prague.

Pacala, S. 1986. Neighborhood models of plant population dynamics. II: Multi-species models of annuals. *Theor. Pop. Biol.* 29:262–92.

Pacala, S. 1987. Neighborhood models of plant population dynamics. III: Models with spatial heterogeneity in the physical environment. *Theor. Pop. Biol.* 31:359–92.

Paine, R. 1966. Food web complexity and species diversity. *Amer. Natur.* 100:65–75.

Paine, R., and S. Levin. 1981. Intertidal landscapes: Disturbance and the dynamics of pattern. *Ecol. Monogr.* 51:145–78.

Park, T. 1936. Studies in population physiology. VI: The effect of differentially conditioned flour upon the fecundity and fertility of *Tribolium confusum.* *J. Exp. Zool.* 73:394–404.

Park, T. 1948. Experimental studies of interspecies competition: I, Competition between populations of the flour beetles *Tribolium confusum* and *Tribolium castaneum.* *Ecol. Monogr.* 18:265–307.

Park, T., E. Gregg, and C. Lutherman. 1941. Studies in population physiology. x, Interspecific competition in populations of granary beetles. *Physiol. Zool.* 14:395–430.

Price, P., et al. 1980. Interactions among three trophic levels. *Ann. Rev. Ecol. Syst.* 11:41–65.

Prout, T., and F. McChesney. 1985. Competition among immatures affects their adult fertility: Population dynamics. *Amer. Natur.* 126:521–58.

Quinn, J., and A. Hastings. 1988. Extinction in subdivided habitats. *Conserv. Biol.* 1:198–208.

Reeve, J., and W. Murdoch. 1985. Aggregation by parasitoids in the successful control of the California red scale: A test of theory. *J. Anim. Ecol.* 54:797–816.

Reeve, J., and W. Murdoch. 1986. Biological control by the parasitoid *Aphytis melinus*, and population stability of the California red scale. *J. Anim. Ecol.* 55:1069–82.

Ricker, W. 1954. Stock and recruitment. *J. Fish. Res. Board Can.* 11:559–623.

Roughgarden, J., Y. Iwasa, and C. Baxter. 1985. Demographic theory for an open marine population with space-limited recruitment. *Ecology* 66:54–67.

Schaeffer, W., and E. Leigh. 1975. The prospective role of mathematical theory in plant ecology. *Syst. Bot.* 1:109–232.

Schoener, T. W. 1972. Mathematical ecology and its place among the sciences. *Science* 178:389–91.

Simberloff, D. 1983. Competition theory, hypothesis testing, and other community-ecological buzzwords. *Amer. Natur.* 122:626–35.

Taylor, L. R. 1971. Aggregation as a species characteristic. In G. Patil, E. Pielou, and W. Waters, eds., *Statistical Ecology,* vol. 1, pp. 357–77. Pennsylvania State University Press, Philadelphia.

Tilman, D. 1977. Resource competition between planktonic algae: An experimental and theoretical approach. *Ecology* 58:338–48.

Tilman, D. 1982. *Resource Competition and Community Structure.* Princeton University Press, Princeton, N.J.

Utida, S. 1953. Interspecific competition between two species of bean weevil. *Ecology* 34:301–307.

Utida, S. 1957. Population fluctuation: An experimental and theoretical approach. In *Cold Spring Harbor Symp. Quant. Biol.* 22:139–51.

Volterra, V. 1931. *Leçons sur la théorie mathématique de la lutte pour la vie.* Marcel Brelot, Paris.

Volterra, V., and U. D'Ancona. 1935. Les associations biologiques au point de vue mathématique. Hermann, Paris.

Chapter 6

Discussion:
Population Dynamics and Species Interactions

DAVID TILMAN

Ecology is the scientific discipline that attempts to determine the causes of patterns in the distribution, abundance, and dynamics of the earth's biota. The earth's ecosystems are complex. In any given habitat, there are tens to hundreds or even thousands of different species. These influence each other both through direct pairwise interactions and through indirect interactions mediated by intermediate species, processes, or substances (Levine 1976; Holt 1977; Vandemeer 1980; Schaffer 1981). Because it is impractical, if not impossible, to observe all the potential interactions among all species and processes, ecological research involves the simplifying assumption that much of the complexity of nature is either unimportant or can be subsumed within a few summary variables. Schaffer (1981, p. 383) defined such simplification as the process of ecological abstraction: "Accordingly, when the empiricist fits data to equations describing the growth rates of particular species, he has, in a sense, 'abstracted' these species from a more complex matrix of interactions in which they are embedded. Nevertheless, because the species studied, as opposed to the variables in the abstracted equations, continue to interact with the remaining, unspecified components of the ecosystem, the parameter values obtained perforce reflect, in part, the species and interactions omitted from the model."

The study of population dynamics and population interactions is, of necessity, a process of ecological abstraction. Ecologists attempt to find, through empirical observation, experimentation, and theory, the critical subset of parameters and interspecific interactions that are needed to describe and predict ecological patterns. How might the process of ecological abstraction best proceed? This paper presents five somewhat related points that may increase the efficiency of ecological research. These musings are based, in part, on discussions at the Asilomar