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THE ROLE OF THEORETICAL ECOLOGY IN THE DESCRIPTION AND UNDERSTANDING OF POPULATIONS IN HETEROGENEOUS ENVIRONMENTS

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The Role of Theoretical Ecology in the Description and Understanding of Populations in Heterogeneous Environments[1]

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SYNOPSIS. The role and function of theoretical ecology are examined. The case is made that theory must be recognized as an activity closely tied to, but separate and independent in objectives and perspective, from field observation and experimentation. Too literal interpretation of models, and rigid insistence on immediate congruence between theory and observation, have led to abuses and distortion of the role of theory. Examples are given to illustrate the partnership between theory and experiment, with emphasis on the partitioning and exploitation of space. The role of theory in guiding understanding and experimentation in the rocky intertidal community of the West Coast (Paine and Levin, 1981) is discussed. Models of individual movement based on random walk assumptions are summarized, with special attention to recent work by Kareiva (1982*a*, *b*, *c*) designed to test the applicability of diffusion models. Such models are shown to provide an excellent foundation for the study of the foraging movements of phytophagous insects: Extensions hold great promise as descriptors of movement for much wider classes of organisms and in the presence of complications such as taxis, grouping behavior, etc. Finally, some brief discussion is given on recent efforts to develop a theory of the evolution of dispersal and dormancy in heterogeneous environments.

INTRODUCTION

Just a few decades ago, theoretical ecology consisted almost exclusively of the works of a few individuals, acknowledged giants who had through force of intellect left their marks upon the subject of ecology. There was no established tradition of theory; hence acceptance of theoretical results met great resistance, and this guaranteed that results which passed the test were of undeniable merit.

Today, the situation has changed drastically. Theoretical ecology is a major growth industry, and the pages of ecological as well as mathematical journals are littered with theory. It thus seems appropriate to begin this discussion by examining the nature of the subject.

The classical view of modeling (Fig. 1) is of an iterative process where model predictions are repeatedly tested against real world observations; the model is eventually either rejected or else modified sufficiently that prediction converges upon observation. This scheme certainly represents an important part of the development of theory, but is much too narrow and constrictive a description to be viewed as the governing paradigm. It suggests a role for the theoretician only in the service of the empiricist, and only with regard to a particular system. It makes no allowance for the vital roles of abstraction and generalization in theory development.

The notion of falsifiability which is implicit in Figure 1 is in the view of many an essential requisite. This view is, however, based on a subordinate and derivative definition of theory; the more basic dictionary definition is that a theory is a systematic statement of principles and methods. The mathematician is familiar with the theory of numbers, the theory of functions, the theory of equations, etc. This is the perception of theory which guides him rather than that of an hypothesis requiring testing. To understand the mathematical theorist, it is necessary to recognize this distinction.

A much more accurate picture is expressed in Figure 2, in which theory and observation are shown as coequal strands, each developing with some degree of independence but drawing strength and inspiration from the other. The differences from Figure 1 are subtle. Figure 2 still implies feedback, as theory affects experiment and conversely; but it leads to a fun-

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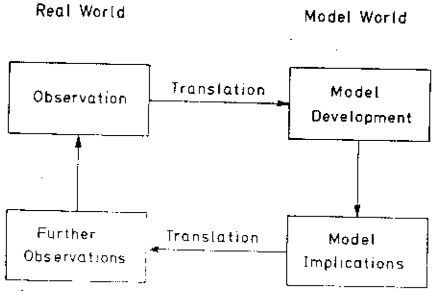

FIG. 1. The interaction between modeling and the real world.

damental distinct view of the progression of science. Theory and observation are separate but equal as intellectual exercises, but sustained in large part by the bridges between them. Constant comparison with the real world and revision of the model are important aspects of the relation of theory to the real world; this was, for example, an essential component of Newton's development of the theory of gravitation, and in general of the Newtonian method (Cohen, 1981). However equally important in Newton's approach was pure deduction, in which attention was restricted to mathematical simplifications (such as the one-body problem) which did not correspond explicitly to physical reality. As Cohen (1981) points out, "The distinction Newton drew between the realm of mathematics, in which Kepler's laws are truly laws, and the realm of physics, in which they are only 'hypotheses,' or approximations, is one of the revolutionary features of Newtonian celestial dynamics."

In that Figure 2 suggests more than just a subservient role for theory, it presents the model which not only the theoretician but also the field biologist should prefer. Theoretical ecology is useful precisely because it offers a new perspective. The development of such perspective requires freedom of inquiry. Without such latitude, the theoretician can operate only within the conceptual framework defined by the empiricist; it should hardly be surprising that such a role is not likely to be attractive to those capable of original ideas. Further, it is a characteristic of theory in many fields that theoretical developments precede application by years or decades. To reject this mode by requiring immediate correspondence to particular situations is to put an unreasonable prior constraint on theory and to encourage excesses in application of theory.

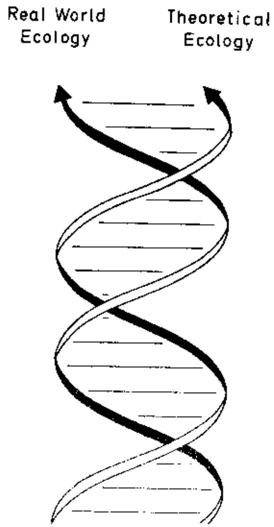

FIG. 2. The interaction between theoretical ecology and the real world.

Certainly, the naturalist may regard as curious the things the theoretician finds interesting. This is reasonable; there is, after all, no accounting for taste. The field biologist should, however, recognize that much of what he chooses to examine may be thought equally obscure by the theoretician. Not every just-so story of natural history is of obvious cosmic importance, and when global significance is removed as a factor and only intellectual value remains, models are intrinsically neither more nor less interesting than membracids. To the theoretician, models are a part of the real world. In studying the logical consequences of assumptions, the theoretician is discovering, not inventing, and is spiritually akin to the natural historian (Levin, 1980*a*).

Both the theoretician and the naturalist must eventually answer to one another. Certainly there must be craft standards within any field; further, a good practitioner in one tradition is sometimes able to judge quality in the other. But the most critical eye should be reserved for the inductive process, by which either the empiricist or the theoretician tries to extrapolate from his own limited studies to derive generalizations about the world beyond. It is in this phase that the most serious abuses occur, and it is here that the most careful scrutiny is justified.

As already suggested, it is by insistence on too literal and immediate a role for theory that overstated claims result. A prime example is provided by an examination of the role of the equations of Lotka and Volterra. These equations, the foundations of the theory of interacting species, have had their value seriously undermined by overuse and by misguided attempts to parametrize them on the basis of data. Such abuses are not to be found in the works of Lotka or Volterra, and obscure the powerful role these equations can and have played as abstractions.

The great mathematician Vito Volterra was enticed into biology by his son-in-law Umberto d'Ancona, a prominent biologist at Padua who interested his father-in-law in the fluctuations of the Adriatic fisheries. To illustrate the possible role of predator-prey interactions in driving population cycles, Volterra (1926) set forth the simplest possible pair of nonlinear equations representing the two species, and showed that with assumptions no more complicated than these, oscillations could result. Of course, the cycles in those "conservative" equations were not stable ones, and inclusion of more complicated nonlinear effects would be necessary to produce stable oscillations. But Volterra's objective of showing how oscillations could arise was best made with the simplest possible example.

In the same spirit, and again using equations in which the per capita rates of growth of species were linearly related to densities, Volterra attacked the problem of competitive interactions. The principle of competitive exclusion, which in its most basic form is predicated upon generalizations of these equations in which growth rates are linearly related to resource density, became crystallized through the work of Volterra. Surely the notion of competitive exclusion was clear in the writing of Darwin and Wallace, and moreover followed from the logic of Malthus. But the importance of the mathematical formalization should not be underestimated; in particular, it inspired the important experiments of Gause (1934). Leibniz (see Newman, 1956; p. 57) is reported to have credited improvements in notation for all of his fundamental contributions to the calculus. While that is clearly an inadequate assessment of Leibniz's worth, it makes the point that if mathematics did nothing more than provide a better notation and means of description, it would earn its keep. But both Leibniz and mathematics have value beyond that.

As already emphasized, the Lotka-Volterra equations should not be taken literally, but as guides to theory, thought, and experimentation. The field biologist asks, "How do species coexist?" thereby using the null hypothesis of competitive exclusion as a tool in sorting out the complexity and diversity of Nature. The theoretician proceeds similarly, using model systems as bases for logical manipulation, in which hypotheses may be posed and their consequences examined. Often such mathematical reasoning is based on equations which do not describe precisely any real system because they by design ignore one or another key aspect. Equations which are made specific to a particular system thereby lose generality (Levins, 1966), whereas equations which abstract the key properties of a wide class of situations are much better vehicles for the development of general theory. Further, in mathematical models the assumptions are exposed, and it is straightforward to modify them singly or in concert to assess the importance of particular factors or mechanisms. Such an approach generally begins from the simplest possible model, which can be made gradually more complicated by the inclusion of greater detail.

This technique can provide access to

some of the most important questions in theoretical ecology. What are the consequences of recognizing that inter- and intraspecific competitive effects vary with time, possibly in response to changes in densities, frequencies, or population structure? What is the importance of stochastic effects on such variation? What feedbacks exist between population dynamics and biogeochemical cycling? What are the implications of recognizing that the generalized Lotka-Volterra equations are overly aggregative and ignore the demographic and genetic compositions of the populations? How does the recognition that populations are distributed over space alter the basic conclusions of theory? The latter question will serve as the focus for the rest of this paper.

SPACE

By exploiting spatial variability, species may foil competitive exclusion. The myriad ways that this can occur and the relations to theory have been reviewed elsewhere (Levin, 1976), and will not be repeated here. Suffice it to say that not only can species utilize underlying environmental heterogeneity through mechanisms of dispersal and dormancy, but also interactions between species can lead to the development of heterogeneity where none existed previously. The potential for coexistence in a heterogeneous environment is orders of magnitude greater than would be possible in a restricted, well-mixed environment.

Associated with an understanding of the importance of space, there are three major and not completely separable questions: (1) How does heterogeneity arise, and how is it maintained? (2) How do species exploit heterogeneity through their patterns of dispersal, dormancy, and growth? (3) How have these patterns of exploitation evolved? In this section, examples of theoretical approaches to these questions are presented.

The nature and development of spatio-temporal heterogeneity

No attempt will be made to review the ways heterogeneity may arise in Nature (but see Levin, 1976; Whittaker and Levin, 1977). It is however obvious that physically defined gradients and microtopographical differences play a fundamental role, and that temporal variation in resource availability adds another dimension. In temporally fluctuating environments dormancy, iteroparity, and other devices to reduce the effects of variation will be favored by natural selection; when neighboring environments fluctuate out of synchrony or at least out of phase with one another, a premium will be placed on mechanisms such as dispersal which average out the effects of spatial variation.

In the rocky intertidal region of the northwestern United States, predation by starfish in the lower part of the middle zone and disturbance by wave stress in the higher portion serve to prevent a potential competitive monopoly by the mussel *Mytilus californianus* (Paine, 1966; Levin and Paine, 1974). The effect of both kinds of stress is to push the system back towards earlier successional stages. Where the starfish *Pisaster* is active, mussels are rare and other species are preeminent. In the higher part of the zone, where *Pisaster* drops out due to limits on physical tolerance, waves open gaps in mussel beds. Mussels are sufficiently abundant there that it is profitable to view the environment as a sea of mussels dotted with islands of opportunity for competitively inferior species (Levin and Paine, 1974, 1975; Paine and Levin, 1981). The opening of a new gap initiates a stochastic succession, and species manage to coexist within the zone through partitioning of the successional gradient; microtopographic differences, variation in timing of disturbance, and chance factors associated with settlement all serve to increase substantially the variety of observed successional sequences and hence the diversity of the system (Paine and Levin, 1981). The gap eventually disappears due to a combination of recruitment of new mussels from the plankton and perimeter encroachment by neighboring mussels.

The importance of such spatio-temporal mosaics has been discussed often in relation to a variety of ecological systems (Watt, 1947; Levin and Paine, 1974; Whittaker and Levin, 1977). Runkle (1979) has utilized the approach of Levin and Paine (1974) as a guide to description of the gap-phase characteristics of some eastern deciduous forests; his work demonstrates the importance of understory trees in exploiting disturbance. Bormann *et al.* (1970) and Bormann and Likens (1979) note the role of spatio-temporal variation in structuring the dynamic mosaic which characterizes the Hubbard Brook ecosystem; they also draw inspiration from the seminal work of A. S. Watt. Elsewhere within northern hardwood forests, similar underlying dynamics but a somewhat different physical regime lead to a different pattern of disturbance: in place of a mosaic, one observes waves of disturbance and regeneration (Sprugel, 1976; Sprugel and Bormann, 1981).

R. T. Paine has studied the rocky intertidal for nearly two decades, and in an early publication (Paine, 1966) documented the critical role of starfish predation. Since 1973, Paine and I have studied intensively the higher portion of the zone. In 1974, we (Levin and Paine, 1974) presented a theoretical model for the structure and dynamics of the system; and that model has served us since to facilitate description, to crystallize thought, and to guide a comprehensive program of experimentation. These, it has seemed to us, are among the most important functions of theory.

Our model is based on the hypothesis of localization: the patch is the fundamental unit of system structure, and the underlying pattern can to a first approximation be described by ignoring the relative positions of patches. This assumption would clearly be inappropriate for a synchronized system such as Sprugel (1976) describes. In the first stage of the model, the population of patches is described according to its demography. The age-size distribution of patches at any time is thereby related to past patterns of disturbance by means of experimentally determined parameters of mussel movement and colonization. This portion of the model leads to excellent agreement with observation except for very small patches, for which stochastic factors assume major importance.

The second part of the model involves study of the patterns of colonization of gaps in relation to their size and age since last disturbance. A generalized sequence of occupancy may be described (Paine and Levin, 1981); but the details of a particular succession are affected by location of the patch, timing of disturbance, and stochastic factors, as well as by patch size.

The study of successional patterns leads naturally to an examination of species exploitation patterns in general; these vary greatly from species to species. For the snails of the genus *Thais*, which reproduce by means of egg cases, movement between patches is part of a foraging regime; many patches will be visited by an individual in a lifetime. For the primary space occupiers, however, the adult will be essentially sessile (as noted, adult mussels may, however, move over short distances and thereby increase resource utilization); for these, movement is a unique event in an individual's life. Barnacles (*Balanus* spp.) define one extreme mode: larvae are dispersed via the plankton over large distances, and nearest neighbor effects are minimized except on a comparably large scale; long-distance dispersal is thus the principal mechanism whereby inter-patch variation is averaged out. For other species, shorter range effects are important: the sea palm *Postelsia palmaeformis* spreads from patch to patch by dispersal of meiospores on the scale of 1–2 m per year (Paine, 1979). However, even *Postelsia* has a longer range mode of dispersal in which the adult sporophyte is ripped from the rocks and transported long distances on the waves. Only rarely will this be an effective mode of transport; but occasionally, the adult plant with its load of spores will find some new haven.

The short range spread of *Postelsia* and the longer range spread of *Balanus* may both be viewed as random walks, modified by prevailing physical forces. Random walk models of movement have received considerable study in the theoretical literature in the form of diffusion models, and represent one of the most exciting points of contact between theory and experiment. In the next section, I briefly review the present status.

Diffusion models of movement

Random models of spread have been of interest to biologists at least since 1911 (Brownlee, 1911), and were studied in detail by population geneticists in the 1930s (Fisher, 1937; Haldane, 1948). Dobzhansky and Wright (1943, 1947) did classic release experiments designed to describe *Drosophila* movement. The most important theoretical paper was that of Skellam (1951), who provided a comprehensive mathematical discussion of the basics of population growth and spread. In the past decade, interest has been renewed in such problems, and an appreciation for the current situation regarding applications to ecology can be obtained from the excellent text of Okubo (1980).

Following the general paradigm introduced earlier, the starting point for the development of theory is with the simplest possible model consistent with biological reality; this mimics the historical development of the subject. It may be that such a simplification will be adequate as a description for few if any populations. However, its assumptions are clear and simple, and additional complications may be introduced as needed.

In this simplest model, the environment is considered constant and homogeneous, and all individuals are identical. Individuals are assumed to undergo random movement between equally spaced points on a line, without bias in any particular direction. In the continuous approximation, in which the lattice points may be thought of as infinitesimally distant from one another, the population density $n(x, t)$ satisfies the *diffusion equation*

$$\frac{\partial n}{\partial t} = D\frac{\partial^2 n}{\partial x^2}, \qquad (1)$$

in which n is the spatial coordinate, t is time, and D is the *diffusion coefficient* (see Okubo, 1980). This model may be immediately generalized to higher dimensions or to allow for the inclusion of growth terms, or to deal with interacting species (Skellam, 1951; Levin, 1974; Okubo, 1980). Skellam introduced the two-dimensional form with radial symmetry and exponential growth

$$\frac{\partial n}{\partial t} = \frac{D}{r}\frac{\partial}{\partial r}\left(r\frac{\partial n}{\partial r}\right) + \alpha n, \qquad (2)$$
$$r^2 = x^2 + y^2$$

to approximate the spread of muskrats in Europe. In a paper which is still influential in the theory of plankton patches (see Steele, 1978), Kierstead and Slobodkin (1953) utilized a similar model to determine critical patch sizes for dinoflagellate blooms. Skellam also discussed the corresponding equation with logistic growth, and the literature in population genetics contains numerous papers concerned with the existence of travelling wave or cline solutions for (1) with a logistic (quadratic) or cubic growth term appended.

Equations (1) and (2) are familiar to mathematicians, since they have arisen in varied applied contexts. Thus the solutions to many of the standard boundary and initial value problems are well-known and may be written down immediately by appeal to classical results. For example, the solution corresponding to a one-time point release of individuals is a normal distribution whose variance in any dimension grows linearly with time at the rate 2D (see Levin, 1978; Okubo, 1980). If boundary effects limit spread, the appropriate modification can be easily computed (Kareiva, 1982*c*). This allows for straightforward testing of the consistency of the diffusion model with observed behavior of released organisms.

Kareiva (1982*a*, *c*), in studying foraging movements in phytophagous insects, has undertaken the most thorough attempt to test the applicability of diffusion models to any group of organisms. He began by setting out plants, equally spaced, in linear arrays and releasing flea beetles (*Phyllotreta* spp.). Using recapture data, he estimated the rate of spread of variance for each species for each spacing used. Those estimates were then used to generate predictions of spread by means of the already mentioned solution of the release model; the predictions were then compared with data using a Kolmogorov-Smirnov test. Agreement was excellent; the diffusion model was acceptable (was not rejected) in almost every case. Dependence of the diffusion coefficient on inter-plant distance suggested a habitat-dependent effect, to which I return shortly.

Kareiva (1982*a*) then conducted a literature survey related to phytophagous insects, examining every case he could find where data were collected in such a way to allow comparison with the predictions of a diffusion model. Situations where baited traps were used were avoided because of known biases such traps introduce. The cases considered represented a wide range of diffusion abilities. Using the same procedure outlined above, he judged seven of the eleven cases to be compatible with the constant coefficient diffusion model.

Most of the exceptional cases showed a leptokurtic distribution, that is, one more peaked than the normal. Dobzhansky and Wright (1943) encountered leptokursis in their original release experiments, and pointed out that this could arise due to heterogeneity of either population or habitat (see also Wright, 1968). Later experiments (Dobzhansky and Powell, 1974) which corrected for population heterogeneity did not show leptokursis.

The usual extension of the diffusion model to take into account spatial variation simply allows the diffusion coefficient to depend on spatial position. In two dimensions, for example, the model becomes

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x}\left(D\frac{\partial u}{\partial x}\right) + \frac{\partial}{\partial y}\left(D\frac{\partial u}{\partial y}\right), \qquad (3)$$

in which $D = D(x, y)$; D could also be allowed to depend upon u or t. However, a diffusion equation derived from a random walk in which emigration is locally determined takes the somewhat different form

$$\frac{\partial u}{\partial t} = \frac{\partial^2}{\partial x^2}(Du) + \frac{\partial^2}{\partial y^2}(Du). \qquad (4)$$

Variant forms are discussed in Okubo (1980). Equation (3) describes a situation in which the properties of the medium determine the rate of diffusion. But (4) is the appropriate limiting approximation for the case of most biological interest: that where an individual "decides" to disperse or not based on local conditions. In experimental studies of insect dispersal in response to varying environmental conditions, one finds as expected that individuals tend to occur in higher densities on more desirable plants (Kareiva, 1982*b*). Such a conclusion is consistent with (4), in which the steady state is one in which u is inversely related to D; it is not, however, consistent with (3), which cannot support a stable nonuniform steady state under homogeneous boundary conditions. Okubo (1980) discusses in further detail the relationships between (3) and (4) and other forms; Dobzhansky *et al.* (1979) use a discretization of (4) to deal with dispersal in heterogeneous environments. A related spatially discrete continuous-time Markov model is utilized by Kareiva (1982*b*) to study flea beetle dispersal in relation to plant quality. De Angelis (1978) also uses a random walk model to study fish distributions in relation to temperature.

The form (4) is formally identical with a model which one would obtain by adding advection to the more classical model (3):

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x}\left(D\frac{\partial u}{\partial x}\right) + \frac{\partial}{\partial y}\left(D\frac{\partial u}{\partial y}\right) + \left(\frac{\partial}{\partial x}(w_x u) + \frac{\partial}{\partial y}(w_y u)\right). \qquad (5)$$

The velocity vector $\mathbf{w} = (w_x, w_y)$ in the more standard development arises from such factors as wind or water; in the present case the identification with (4) is made by setting $\mathbf{w} = \text{grad } D$, so that the variation in the diffusion coefficient drives the population towards environments with lower D.

Other modifications of the diffusion model have also been considered. Several authors (Gurney and Nisbet, 1976; Gurtin and MacCamy, 1977; Shigesada *et al.*, 1979; Aronson, 1980; Namba, 1980; Mimura, 1981; Newman and Sagan, 1981) have dealt with models in which emigration is keyed to density; experimental support for such responses may be found in the works of Morisita (1950, 1954), Ito (1952), Kono (1952), Wantanabe *et al.* (1952), Taylor and Taylor (1977), and Kareiva (1982*a*).

Other extensions of the diffusion model incorporate taxis (Keller and Segel, 1971), correlations between steps (Goldstein, 1951; Patlak, 1953; Okubo, 1980; see also Jones *et al.*, 1980), and grouping of various kinds (Sakai, 1973; Okubo and Chiang, 1974; Okubo *et al.*, 1977).

The strength of the diffusion approach is that it is flexible; additional complications in assumptions (for example, spatial heterogeneity) are accommodated fairly easily. The malleability might be deemed a weakness in that although particular models are in theory testable the general approach is not. However, this is exactly the mode of operation suggested by Figure 2. There are strong bridges between theory and experiment, as represented by cases where specific diffusion models can be shown to be good descriptors; these provide a sound foundation for the beginning of a study of dispersal, and specifically for extensions which build on the diffusion model. Obviously, not every situation is appropriate to such a model; but a wide variety are. Drawing incentive from field situations, the theoretician develops the appropriate more complicated models, incorporating advection, spatial dependence, taxis, etc. Because more parameters are involved, it becomes harder and harder to test such models. Nonetheless, even unverified, such theoretical extensions can make important contributions to interpretation and understanding, and to experimental design (see for example Dobzhansky *et al.*, 1979; Kareiva, 1982*a*, *b*, *c*). It is usually possible to generate qualitative predictions from them, and to use them as bases for simulations which can be compared with data. Although such comparisons do not constitute tests, they may lead to model rejection or alternatively to increased confidence in the usefulness of the model; this confidence is subject to constant reevaluation as new data become available. Possibly, the methods eventually may be found to test the more complicated models. In other cases, however, the limitations of experimental methodology may make testing impossible, at least for the present. It would be foolhardy to restrict the usage of models to those situations where they have been substantiated. An important role for theory is in dealing with cases for which testing is impossible, perhaps because of the state of basic methodology, but perhaps simply because one cannot risk experimentation with the system of interest. The application of theory to real world problems is an attempt to utilize the power of models to generalize so that educated guesses may be made either on the basis of extrapolation from situations where the model has been tested, or else by the argument of consistent logical development. It follows that there must be pieces of theory which cannot yet be supported by empirical evidence and have thus not been tested. Whether such pieces of theory are in theory testable is irrelevant as well as untestable.

Evolutionary strategies

Dispersal is one of several mechanisms by which organisms deal with environmental variability: others include dormancy and iteroparity. The evolution of such strategies involves both density and frequency dependence, and hence optimization arguments are inappropriate except in the limited sense of evolutionarily stable strategies (Maynard Smith, 1976; Levin, 1980*b*; Levin *et al.*, 1982).

There is a sizeable literature in population genetics associated with the consequences of dispersal, but only recently have attempts been made to view the evolution of dispersal strategies from an ecological perspective (Gadgil, 1971; Reddingius, 1971; Strathmann, 1974; Roff, 1975; Hamilton and May, 1977; Motro, 1979*a*, *b*; Comins *et al.*, 1980; Levin, 1980*b*; Levin *et al.*, 1982). The theoretical approach has been to consider competition between different morphs and either to incorporate explicit assumptions concerning the correspondence between genotype and phenotypes, or to assume that an evolutionarily stable type will be achieved. In relation to the considerations of this paper, the primary question addressed in those

studies concerns what fraction of one's energy to commit to dispersal, with attention generally restricted to situations (*e.g.*, larval or seed or pollen dispersal) in which dispersal occurs basically once in a lifetime.

For the most part, theoretical treatments of dispersal have been very general and qualitative. This is to be expected in the early development of a theory; a general framework has to be constructed. Moreover, many of the data that are critical to the evaluation of such theories are not available: the costs associated with dispersal structures, the genetic basis of dispersal, the patterns of environmental variability, population heterogeneity regarding dispersal characteristics, the relationship between morphology and dispersal capability, etc. However, the presentation of an initial theory can allow identification of critical variables, and in this way help shape experimentation and data collection. Those data can then be compared with the predictions of more specifically tailored second generation models, and eventually theory and data can be brought into closer contact. For example, with several collaborators I have been developing a variant on the model given in Levin *et al.* (1982) to deal with the evolution of dispersal and dormancy strategies in common ragweed; and Ellner (unpublished) has proceeded similarly in trying to relate adaptations for dispersal in species of the genus *Picris* to environmental gradients. In general, given the recent interest and activity in the area it is to be expected that the next several years will show rapid progress in the development of a theoretical basis for understanding dispersal and dormancy.

CONCLUSIONS

I have tried to show, by general argument and by case studies, how theory and empiricism interact. Models may in some instances be taken literally and used for prediction, but their more usual and more powerful role is metaphorical: as organizers of thought, as aids to explanation, and as guides to experimental design.

Consideration of the effects of space has led to some of the most profitable interactions between theory and experiment. In particular, data on small-scale movements of phytophagous insects show remarkable agreement with theoretical models of population diffusion in homogeneous and heterogeneous environments. Diffusion models have been favored by theoreticians for a half century or more, but until recently there have been few attempts to test their applicability; as in other areas of science, theory has had to be developed in the absence of critical data, and has preceded by many years the collection of those data. However, the theory of dispersal is now in a very healthy state, with strong points of contact between theory and experiment. New theory is being developed with strong motivation from biological observation, and an exciting symbiosis has developed.

In other areas where theory is being developed, the points of contact will be less evident, and more latitude is essential. The biologist must recognize the intellectual validity of the well-performed theoretical exercise, and must have confidence that there will be profitable, perhaps accidental, fallout at some time in the future. In not recognizing this and in insisting on more immediate evidence of application, one runs the risk of forcing exaggerated claims meant to demonstrate relevance. This is in the interest neither of field biologists nor of theoreticians, and not surprisingly has led at times to anti-theoretical backlash.

In answer to the main question posed by this symposium, within the broadened perspective defined by Figure 2, theoretical ecology has a great deal to contribute to our understanding of the real world. But an appreciation of that contribution requires a recognition of theory development as an activity closely tied to, but separate and independent in its objectives and perspective from, field observation and experimentation.

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