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The strategy of "The strategy of model building in population biology"

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Abstract In this essay, I argue for four related claims. First, Richard Levins' classic "The Strategy of Model Building in Population Biology" was a statement and defense of theoretical population biology growing out of collaborations between Robert MacArthur, Richard Lewontin, E. O. Wilson, and others. Second, I argue that the essay served as a response to the rise of systems ecology especially as pioneered by Kenneth Watt. Third, the arguments offered by Levins against systems ecology and in favor of his own methodological program are best construed as "pragmatic". Fourth, I consider limitations of Levins' arguments given contemporary population biology.

Keywords Richard Levins · Robert MacArthur · Population biology · Ecology · Systems ecology · Model Building · Tradeoffs

Introduction

This essay is an historical exploration of the methodological underpinnings of Richard Levin's classic essay "The Strategy of Model Building in Population Biology" in which I argue for several theses. First and foremost, his essay constitutes a statement and defense of a more "holistic and integrated" theoretical population biology that grew out of the informal and formal collaborations of Levins, Robert MacArthur, Richard Lewontin, E. O. Wilson, and others. Second, Levins' essay and the views introduced would be used as a response to the rise of systems ecology in the 1960s against the background of the International Biological Program. Third, the arguments Levins employs are best construed as "pragmatic"—a point that is sometimes unnoticed by contemporary scientists and philosophers. Finally, I turn to the contemporary and consider the similarities and differences between the limita-

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tions of population biology of the 1960s and that of 2006 raising open questions about the applicability of Levins' analysis.

"Simple theorists" or a prolegomena to a new population biology

In the 1960s, Levins, Richard Lewontin, Robert MacArthur, E. O. Wilson, Leigh Van Valen, and others were interested in integrating different areas of population biology mathematically. Apparently they met on several occasions at the MacArthur's lakeside home in Marlboro, Vermont discussing their own work in population genetics, ecology, biogeography, and ethology and how a ''simple theory'' might be devised.[1] Fig. 1

In an interview in the early seventies, E. O. Wilson describes the methodological program of the ''simple theorists'',

> Biologists like MacArthur and myself, and other scientists at Harvard, Princeton, and the University of Chicago especially, believe in what has come to be called ''simple theory'', that is, we deliberately try to simplify the natural universe in order to produce mathematical principles. We think this is the most creative way to develop workable theories. We don't even try to take all the possible factors in a particular situation into account, such as sudden changes of weather or the effects of unusual tides. (Chisholm 1972: 177)[2]

He goes on to compare this program against the competition,

> On the one hand, you've got the hard ecologists like MacArthur and myself, who, as I've explained, believe in simplifying theory as much as possible.

Fig. 1 Richard Levins and E. O. Wilson in Florida in the 1960s (from Chisholm 1972)

[1] E. O. Wilson (1994) has written about the meetings that occurred; however, little has been written on the substance of those meetings.

[2] At the time, MacArthur was at Princeton and Lewontin and Levins were at the University of Chicago.

> You can call us the simple theorists. But in the last five years or so a group has developed, around people like Paul Ehrlich at Stanford, C. S. Holling at British Columbia in Canada, and Kenneth Watt at Davis, who are also mathematical ecologists, but who believe in complex theory... They say that because ecosystems are so vastly complex, you must be able to take all the various components into account. You really must feed in a lot of the stuff that we simple theorists leave out, like sunsets and tides and temperature variations in winter, and the only way you can do this is with a computer. To them, in other words, the ideal modern ecologist is a computer technologist, who scans the whole environment, feeds all the relevant information into a computer, and uses the computer to simulate problems and make projections into the future. (Chisholm 1972: 181–182)

In recent interviews, Richard Lewontin also has discussed the work of the ''simple theorists'':

> ...Dick Levins and I had hooked up with Robert MacArthur, who was then at Penn but then went to Princeton, and the three of us had this idea that we ought to be able to build a science of population biology that would fuse the intrapopulation genetic variation aspect of biology with demography and population ecology, and so on... Dick Levins and I and Robert MacArthur used to meet, and we had a sense of really building some new science of population biology. We had contact with Ed Wilson, who was also interested in that, and with Lee Van Valen. We met a couple of times in Vermont at Robert's 'in-laws' place and, in general, had a kind of zeal for founding a new field. (Singh et. al. 2001: 37)

He goes on to discuss the work of Levins, MacArthur, and Wilson in the context of this new program.

> As you can imagine those were intellectually heady days for all of us. Dick's book on *Evolution in Changing Environments*, which was an extension of his thesis, was published. That book became extremely well-known, again, as the first attempt to solve problems of evolution in varying environments in a systematic way that did not necessarily involve manipulating gene frequencies but working at a somewhat higher level. And in his work with MacArthur, and then the MacArthur and Wilson theory of biogeography, all was part of one big movement that was largely centered at Chicago because of all the money we had, but which had as outliers Princeton and the unique elements at Harvard with Ed Wilson and Bossert. (Singh et al. 2001: 37)

As a product of the collaborative work of these biologists, we were offered models of environmental heterogeneity (Levins 1968), density-dependent selection (Lewontin 1965; MacArthur 1962, 1965), limiting similarity (MacArthur and Levins 1967), and equilibrium island biogeography (MacArthur and Wilson (1967). I contend that Levins' 1966 essay is a methodological statement and defense of this research program. Let's now turn to the content of that essay.

In Levins' 1966 paper, there are three especially significant contributions. First, there is much discussed topic of the tradeoffs in biological modeling. Second, there is a discussion of robustness analysis. Third, there is a presentation of the notion of a sufficient parameter. In this essay I will focus on the first contribution since it is most intimately connected to his criticisms of systems ecology.[3]

Levins noted in the essay that traditional theoretical population biology typically is composed of ''traditionally independent clusters'' of population ecology, population genetics, ethology, and biogeography. Moreover, the models of these respective disciplines concern very different state variables and parameters. For example, population ecological models were devised to describe ''multi-species systems described in terms of their demographics and population densities'' (1966: 421). The models ignored change in gene frequencies; i.e., evolution. Similarly, population genetic models were devised to represent ''change in genotype frequencies as a function of natural selection, inbreeding, mutation, migration and random genetic drift'' (1966: 421). However, in these microevolutionary models, the environment is assumed to be mostly unchanging.

Levins contends however that ecological and evolutionary processes are temporally ''commensurate'' (1966: 421). For example, in his later essay ''The Limits of Complexity'' (1973: 111), he argues that (a) speciation in a century or two, (b) evolution of heavy metal tolerance in plants, (c) insect adaptation to insecticides like DDT, and (d) species turnover on islands in Florida and the Caribbean all show that ecological and evolutionary processes occur on overlapping timescales. If ecological and evolutionary processes are temporally commensurate, then these different processes may interact with each other dynamically. One cannot separate G. E. Hutchinson's ''evolutionary play'' and ''ecological theatre'' in the customary temporal way.

> Thus population biology must deal simultaneously with genetic, physiological, and age heterogeneity within species of multispecies changing demographically and evolving under the fluctuating influences of other species in a heterogeneous environment... The ''naïve, brute force approach'' would be to setup a ''one-to-one reflection of this complexity'' (1966: 421).

However,

> This would require using perhaps 100 simultaneous partial differential equations with time lags; measuring hundreds of parameters, solving equations to get numerical predictions, and then measuring these predictions against nature. (1966: 421)

We can see the sort of program that Levins had in mind by considering the diagram made famous in Isadore Nabi's ''On the Tendencies of Motion'' (Levins and Lewontin 1985).[4] Here we see a ridiculously complex and amusing flowchart of systems ecology style modeling. Fig. 2

First, he argues first that there are ''too many parameters to measure'' only ''vaguely defined'' which would ''require a lifetime'' to measure (1966: 421). Second, the equations would be analytically insoluble and would ''exceed the capacity of

[3] It is unfortunate that the discussion of Levins' work has largely focused on the issue of tradeoffs in biological modeling since robustness analysis and the notion of a sufficient parameter are also philosophically important. Philosophers such as Bill Wimsatt and Michael Weisberg have and are correcting that tendency.

[4] 'Isadore Nabi' was a penname under which Richard Lewontin, Richard Levins, and probably others infamously wrote under in 1960s and 1970s.

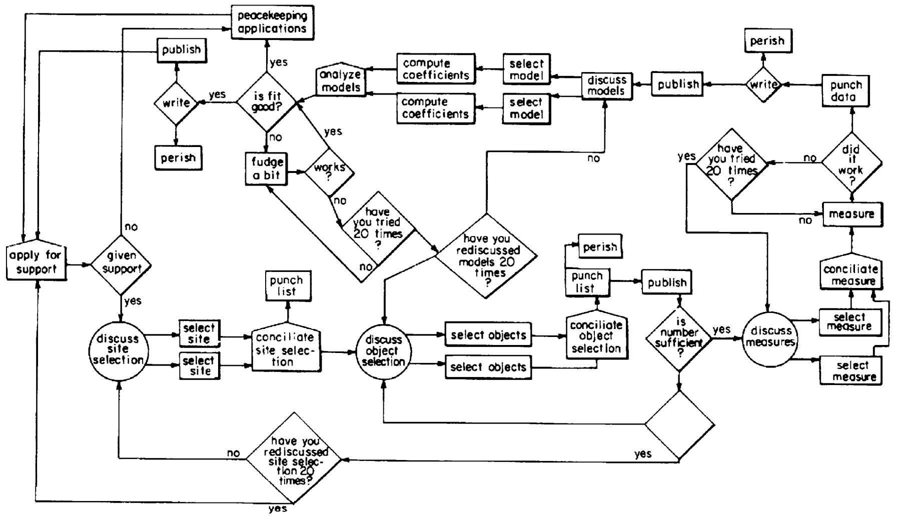

Fig. 2 "Nabian" flowchart of systems analysis

even good computers" (1966: 421). Third, the results of would be expressed in terms that would have "no meaning for us" (1966: 421). He continues,

> It is of course desirable to work with manageable models which maximize generality, realism, and precision toward the overlapping but not identical goals of understanding, predicting, and modifying nature. But this cannot be done. (1966: 422)

Levins suggests that population biologists have arrived at three strategies (at least) for building models to cope with these complexities.

Type I models: Generality is sacrificed for precision and realism
Type II models: Realism is sacrificed for generality and precision
Type III models: Precision is sacrificed for generality and realism

He writes, "Thus a satisfactory theory is usually a cluster of models" (1966: 431) and we should look for a "robust theorem which is relatively free of the details of the model" (1966: 423). Levins famously concludes that "our truth is the intersection of independent lies" (1966: 423). We can see the sort of "cluster" Levins had in mind when we considered this holistic and integrated theoretical population biology. Fig. 3

Given the above discussion, I suggest that Levin's argument is most charitably interpreted as the following:

1. An optimally general, precise, and realistic model would require using a very large number of parameters in a very large number of simultaneous partial differential equations.
2. If a model is of this form, then the equations would be analytically insoluble, uninterpretable, and unmeasurable.
3. If the equations are analytically insoluble, uninterpretable, and unmeasurable, then clearly the model is of little use to scientists.

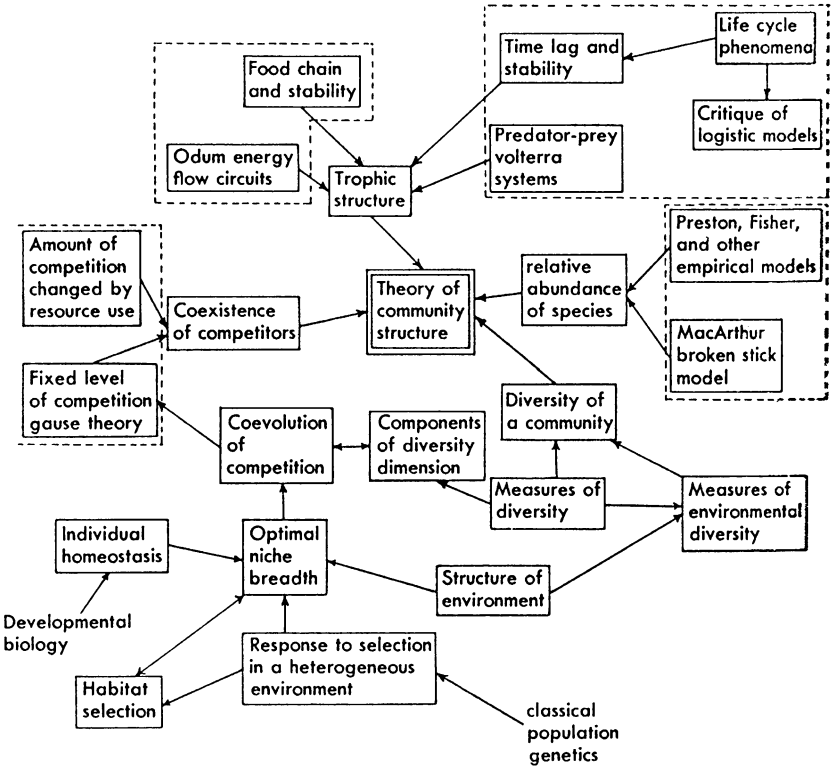

Fig. 3 Population biology's cluster of models circa 1966

4. Therefore, there is an unavoidable trade-off for us between the generality, precision, and realism of the mathematical models if they are to be of any use to evolutionists and ecologists.

It is crucial to note that the problems of insolubility, uninterpretability, and unmeasurability are all problems that arise as products of scientists *and* their models, and *not* from the models alone. The inability to use insoluble equations even with good computers, the inability to interpret an unwieldy mathematical formalism, and inability to carry out all of requisite measurements are all functions of our limitations along with the biological systems of interest. In §IV, I will defend this interpretation of Levins' argument with more textual evidence, and in §V we will consider the soundness of this argument. However, let's turn to the "Simple Theorists" opposition and consider Levins' critique.

The International Biological Program and FORTRAN Ecology[5]

To better understand Levins' essay, we must begin by considering one of the most significant organizations developed to deal with biological systems and the

[5]My discussion of the International Biological Program comes from Bocking (1997), Golley (1993), and Kwa (1987) and readers looking for detail and discussion should consult these sources.

problems concerning them. The International Biological Program was first conceptualized in Europe in the 1950s and was officially launched in Amsterdam in 1961. From 1970 to 1974, The US Congress provided $40 million to the American IBP with five ''biome studies'' involving the computerized modeling of large scale ecosystems and some smaller scale projects. The most prominent were the Eastern Deciduous Forest Biome directed by Stanley Auerbach in Tennessee and the Grassland Biome in Colorado directed by George Van Dyne. The IBP was officially terminated in July of 1974 though many of the larger projects continued to receive significant funding.

In 1951, Eugene Odum—a major proponent of the IBP and ecosystem ecology - carried out his first contract research with the Atomic Energy Commission. As a consequence of his and other contacts with the AEC, ecosystem ecologists had an influence on Washington politicians. In 1963, the Ecological Society of America created an IBP committee with Odum as its chairman with the purpose to convince the National Academy of the Sciences to nominate ecologists to the National Committee for the IBP. Eventually they attracted the attention of Congress and specifically the House of Representatives to hold hearings in 1967 on the possibility of Congress providing support for the IBP. Congress came to believe that the IBP and ecosystem ecologists could use their ''cybernetic program'' to solve important applied environmental problems. Stanley Cain, the Assistant Secretary of the Department of the Interior for Fish, Wildlife, and Parks wrote,

> IBP is really the world's first organized effort to face up to this class of vital problems that deal with the limits of natural productivity in various ecological systems. The possibilities of management of such systems extend before us new frontiers that can be reached if we develop and apply ecological knowledge. (Kwa 1987: 424)

Eugene and Howard Odum had used effective metaphors for presenting ecosystem ecology to the public and government; specifically that of a ''cybernetic machine'' or program (Kwa 1987; Taylor 1988). However, in addition, they both believed that to develop ecosystem ecology, they would need to use the new mathematical tools of systems analysis to bring this approach to fruition. Kenneth E. F. Watt would be just the person for the job.

In the 1950s, mathematical ecologist Kenneth E. F. Watt worked for the Statistical Research Service of the Canadian Department of Agriculture after having left the RAND Corporation. Fig. 4. Most significantly, Watt had worked on the Spruce Budworm infestation in Northern Ontario. He would become the spokesperson for the integration of ecosystem ecology and systems analysis (Palladino 1990: 229).

Watt was convinced that traditional ''analytical'' ecological models were doomed to fail since they were terribly unrealistic given the exceedingly complex nature of ecosystems (Palladino 1990: 227–228; Watt 1962, 1966).[6] Moreover, one must study entire systems since he believed one cannot ''decompose'' their dynamics into the properties of their parts. From his point of view, given the new powerful computers and programming languages like FORTRAN, one could combine system analysis with ecosystem ecology and thus have *systems ecology*.

[6] In this context, ''analytical models'' are the traditional Lotka-Volterra models that ecologists had been using. They need not admit of closed form solutions.

Fig. 4 Kenneth E. F. Watt

Watt's methodology involved four components: measurement, analysis, description, and simulation.

A. Measurement: Determine "...a list of variables and causal pathways that seem of potential importance in determining the function of the system" (1966: 7).
B. Analysis: "After all the variables provisionally thought to be important have been measured, it is necessary to evaluate the real relative importance of the various variables..." using multiple regression and analysis of variance (1966: 8).
C. Description: "After it has been determined which variables need to be included in a systems model by using multiple analysis of variance and multiple regression analysis, it is necessary to structure the important factors into a model" (1966: 9).
D. Simulation: "Once a model has been developed which accurately describes the behavior of a complex system, it can be used in simulation studies to show the system can be manipulated in real life to produce a result optimal to man" (1966: 9).

Given more powerful computer technologies, Watt believed that systems ecology could "transcend" the analytical approach of traditional population and community ecologists (Palladino 1990: 229).

In 1968, Levins' "Ecological Engineering: Theory and Technology"—a review of Watt's *Ecology and Nature Resource Management*—appeared in *The Quarterly Review of Biology*. Levins recognized the need for ecologists to work on applied problems; however, he argued that any such attempt must satisfy several criteria.[7] He writes,

> It must be holistic, treating complex systems as systems. It must be interdisciplinary, combining the experience of population ecology with results from population genetics, bioclimatology, and those aspects of physiology and development which are relevant to individual adaptation. It must be theoretical

[7] In an interview E. O. Wilson considers the "political argument" of the systems ecologists. "Their political argument is that all ecologists should harness themselves to the movement of applied ecology, plotting the management of the world's fisheries, re-routing water systems, managing the world's forest and so on. To me, these are social engineering problems, and there's not much ecology in them. There are basic ecological *principles* involved, but that's all" (Chisholm 1972: 181). It is not clear that Wilson would stand by this line of argument given his work over the last few decades.

> attempting to develop a frame of reference for interpreting the dynamic complexity of ecosystems. And it must have a conscious strategy of research with special attention paid to the ways of coordinating theoretical and observational work. (1968: 302)

Levins argues that Watt's approach fails on each score.

Considering ''holism'', he writes that Watts ''...tried to deal with complex wholes but without using any of the properties of complex systems'' (1968: 304). For example, he notes that Watts does not study ''the connectivity of a food web, the breadth of a species' niche, the patchiness of the environment... However, Watt prefers photographically exact models in a one-to-one correspondence with the object of study. (1966: 304) Considering theory, Levins argues that he construes theory ''in its narrowest sense only'' involving ''sophisticated curve fitting'' (1968: 302). Finally, considering Watt's interdisciplinary research, he argues that Watt ignores a ''rich literature'' on various topics and that his ''frame or reference'' made this ''virtually inevitable''. Moreover, the environmental it treated only in ''its most elementary form, as data'' (1968: 303).

Levins recommends an alternative strategy; the very one that had already been discussed in his classic 1966 paper. He writes,

1. An effective theory of population biology must have strong cross links to bioclimatology, developmental biology (in relation to individual phenotypic flexibility), genetics (since microevolutionary time overlaps with demographic time) and niche theory.
2. Theory must be developed simultaneously at several levels from the greatest generality (and low precision) to the narrower and more precise interpretation of particular species.
3. No single model can meet all the requirements of generality, realism, precision, and manageability. Therefore we need a cluster of models. Some will be alternative models of the same situation, aimed at testing the robustness of the conclusions to changes in the details of the assumptions. Other will be arranged hierarchically, the contained models accounting for the parameters which are taken as given for the higher levels.
4. The premature use of numerical methods (especially computer methods) can often confuse numbers with knowledge. Therefore analytical and qualitative techniques should be pushed as far as possible before computers brought in. In particular, it would be destructive if modern systems ecologies were to be identified with ''computer ecology'' or ''Fortran ecology''. (1968: 504)

In Levin's 1968 response to Watt, we see the re-articulation of a methodological program that would serve as an alternative to systems ecology. The fact is that Levins' review is an *application* of the themes discussed in his 1966 paper and his 1968 monograph *Evolution in Changing Environments.*

Paulo Palladino writes,

> I have argued that the population biologist Richard Levins, prompted by these institutional developments, sought to challenge the social position of systems ecology, and to assert the intellectual priority of theoretical population ecology. He attempted to do so by articulating a nontrivial and rather carefully thought out classification of ecological models that lead to the disqualification

> of systems analysis as a legitimate approach to the study of ecological phenomena. (1990: 242)

There are several problems with Palladino's claims. First, Levins did seek to challenge systems ecology and its ''social position''; however, his classification of models clearly had been articulated *prior to* his review of Watt's book. Thus, the methodology articulated by the ''simple theorists'' was *applied* by Levins in his review rather than being articulated simply for the purpose of criticizing systems ecology. Second, the target of Levins' 1966 article is ultimately *model monism*—that there is a single correct model type for successfully representing evolutionary-ecological systems. Physicists-turned-ecologists like Egbert Leigh and system ecologists like Watt are all under criticism *if* one accepts that Type I or Type II models are the *only* model types one should use. Palladino ignores Levins' model pluralism when he writes, ''According to Levins, the last class, that of general and realistic models, like his own, was the only one deserving the attention of biologists'' (1990: 231).[8] Thus, Levins' essay is not simply a sociopolitical response to systems ecology, but is embedded in a larger refocusing of the science of population biology on a more methodologically sound pluralistic strategy. We can now turn to the nature of Levin's claims.

The pragmatics of modeling

Levins was not arguing for a logical tradeoff in biological modeling. As I argued in §I, his argument is pragmatic—it concerns our limitations, our aims, *and* the complexity of biological systems (Odenbaugh 2001).[9] This pragmatic interpretation I suggest is evidenced both by passages from the 1966 paper, but from other work as well. Here are some passages from his *Evolution and Changing Environments*.

> The attempt to consider genetic, demographic, environmental, and interspecific differences simultaneously immediately runs into technical difficulties. A precise mathematical description may involve hundreds of parameters, many of which are difficult to measure, and the solution of many simultaneous nonlinear partial differential equations, which are usually insoluble, to get answers that are complicated expressions of the parameters which are uninterpretable. (1968: 5)

> Suppose that we did know the interrelations among all parts of a system and would describe the rate of change of each variable as a function of the others.

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[8] Historian Sharon Kingsland correctly notes Levins' pluralism; however, she writes, ''Of course [Levins] realized that the choice of different strategies would reflect conflicting goals and even conflicting aesthetic standards on the part of biologists. For this reason he regarded disagreements about methods as basically irreconcilable'' (1995: 190). However, Levins would not have regarded them as irreconcilable. In his discussion of types of ''imprecision'', he writes that ''general models are necessary but not sufficient for understanding nature. For understanding is not achieved by generality alone, but by a relation between the general and the particular'' (1966: 430). Thus, this suggests that successful explanation of the phenomena *requires* multiple models or what Levins calls ''clusters of models''.

[9] By 'pragmatic', I am suggesting that Levins was not focusing on the syntactical or semantic features of models per se, rather, he is focusing on the use of these representations and the constraints involved. This is also not to claim that there are not logical or mathematical tradeoffs in biological modeling (see Odenbaugh, J. and M. Weisberg, unpublished: Desiderata in Tension).

> Then we would have a very large set of simultaneous nonlinear equations in a vast number of variables, and depending on so many parameters, the estimation of each of which may take a lifetime. These equations will usually be insoluble. They would be likely to be too numerous to compute. If we could compute, the solution would be simply a number. If we could solve the equations the answer would be complicated expression in the parameters that would have no meaning for us. Therefore the only way to understand a complex system is to study something else instead. That something is a model. (1968: 75)

Interestingly, Levins in other work has been exceptionally clear in drawing a distinction between the complexity of biological system and the epistemological and methodological implications of such complexities. In his ''Limits of Complexity'', Levins writes,

> Yet we have the curious fact that [complex] systems are intelligible, far more so than if they were totally interacting... Accounting for the intelligibility of complex systems is both an ontological problem and an epistemological one. We want to know both how an arbitrary complex system behaves, and how this affects our study of it (1973: 113).

Similarly, in ''Complex Systems'', he writes:

> We are concerned with two interrelated problems – the ontological issue of how such systems are really put together and the epistemological one of how to study and describe them. Clearly our epistemology must be based on the ontology, but the correspondence between the complexity of the system and the tools for dealing with it is not one-to-one or monotonic. Clearly, a [totally complex] system of this type would be unknowable...The totally complex system corresponds to a trivial epistemology which is impotent. (74)

As examples of the misinterpretation often given of Levins' discussion of tradeoffs, consider the work of Paulo Palladino and Steven Orzack and Elliott Sober respectively. Palladino writes, ''[Levins] went on to claim as a self-evident truth that no model could exhibit all three features; at most, he argued it could meet two of these criteria'' (1990: 230). He continues, ''However, there is no a priori reason for Levins' assertion that no model can be simultaneously realistic, precise, and general'' (1990: 231). The fact that Levins nowhere gives an ''a priori reason'' for claims about tradeoffs is no problem since there is good textual evidence that he did not believe it to be ''self-evident'' that such tradeoffs exist. Rather, the passages cited suggest that Levins took the tradeoffs to be determined by the properties of the models themselves and contingent properties of us as scientists. Thus, claims about this tradeoff could neither be self-evident nor known a priori since the tradeoff is contingently true at best.

Similarly, Orzack and Sober write, ''Levins does not define any of the model properties that he discusses, nor does he provide an argument for why they are mutually antagonistic'' (1993: 534). It is unfortunately true that Levins does not define the model properties of generality, realism, and precision. However, as we have seen, Levins does not claim that the model properties are mutually antagonistic per se; rather, the evidence suggests that he took the antagonism to concern the relationship between the models, the properties of biological systems, and our psychological and computational limitations. However, one can contend that there are passages where Levins refers to a logical tradeoff amongst model properties.[10]

> The multiplicity of models is imposed by the contradictory demands of a complex, heterogeneous nature and a mind that can only cope with few variables at a time; by the contradictory desiderata of generality, realism, and precision; by the need to understand and also to control; even by the aesthetic standards which emphasize the stark simplicity and power of a general theorem as against the richness and the diversity of living nature. These conflicts are irreconcilable. (1966: 431)

It is true that Levins uses the phrase ''contradictory desiderata'' which suggests there might be a tension between model properties alone. However, first it is important to note that in the very same paragraph Levins mentions the ''contradictory demands'' between a complex nature and human minds. Second, Levins is a Marxist and Marxists use the term 'contradiction' in a different sense than simply a proposition that is logically inconsistent. Thus, given the amount of textual evidence suggesting a pragmatic interpretation, I suggest that the logical or semantic interpretation is less charitable to Levins' claims.[11]

Thus, with some cases notwithstanding, Levins' discussion of tradeoffs in biological modeling concerns the tension between our own limitations with respect to what we can compute, measure, and understand, the aims we bring to our science, and the complexity of the systems themselves. Let us now turn to open questions concerning whether Levins' was correct.

Back to the future

There are several worries that arise when assessing Levins' views concerning the limitations of population biology. First, it is true that many models in the biological sciences do not have closed form solutions. However, it does not follow that these models will be useless from the fact that they do not admit of closed form solutions. Rather, it is our computational abilities that must be augmented. From 1966 to today, we have augmented our computational abilities through simulations by inductively exploring the behavior of models and then find regularities or patterns in the model's behavior. In fact, since Levins' essay there has been tremendous progress in modeling populations and communities with what are called *individual based models*.

Traditionally ecologists have used what are called *p*-state models which are built on the *identical individuals assumptions*—namely that individual organisms are *nearly* identical in their genetic and demographic properties. Models like the Lotka-Volterra predatory-prey equations are premised on this assumption through use of the law of mass action since their interactions are proportional to their abundance alone. On the other hand, what are called *i*-state models do not make the identical

[10] I am indebted to Steven Orzack (2005) for raising this worry.

[11] Some have misunderstood the claims of Odenbaugh (2001). In that essay, I argued that Orzack and Sober had misinterpreted Levin's claims about tradeoffs in biological modeling. However, I did not intend to defend the empirical claim that such tradeoffs exist; rather, I did intend to show that Orzack and Sober's argument that they do not exist was fallacious.

individuals assumption. For example, with *individual distribution models*, individual organisms are placed in different classes based on differences in age, sex, or size. *Individual configuration models* represent the changes of each individual organism through computer simulations. Many proponents suggest that individual based models are general, realistic, and precise (Odenbaugh 2005). Thus, it seems that *our* powerful computer technologies might have invalidated Levins' critique.

Second, if a model is so complex as to be uninterpretable, then it will be useless. However, are the equations in population biology this complex? It is true that models often have a large number of distinct variables and parameters. For example, suppose we are modeling the interactions between species in an ecological community. One customary way of doing this due to Levins (1968) is through a *community matrix*. The matrix is composed of interaction coefficients α_{ij} which represents the per capita effect of species *j* on species *i*.

$$\begin{bmatrix} \alpha_{1,1} & \alpha_{1,2} & \cdots & \alpha_{1,30} \\ \alpha_{2,1} & \alpha_{2,2} & \cdots & \alpha_{2,30} \\ \vdots & \vdots & \ddots & \vdots \\ \alpha_{30,1} & \alpha_{30,2} & \cdots & \alpha_{30,30} \end{bmatrix}$$

If we have a community of thirty species for example, then our matrix will have $30 \times 30 = 900$ distinct elements.[12] However, this is true only if we count *tokens* but not *types*. There are 900 distinct tokens of the type—for example, $a_{5,}$ a_{15}—but only one type, a_{ij}. Surely we can understand what the matrix represents.

Third, the problem of interpretation appears to be dependent on the form of representation used. To see this, let's consider the simplest population growth model with age structure. Let $N_i(t)$ represent the number of individuals at *t* in age class *i* of with *k* age classes in the population. Let P_i be the probability an individual in *i* survives to $i + 1$ and F_i be the average number of offspring produced by an individual of *i*. If there are *k* age classes, then we have the following set of equations:

$$\begin{aligned} n_1(t+1) &= F_1 n_1(t) + F_2 n_2(t) + \cdots + F_k n_k(t) \\ n_2(t+1) &= P_1 n_1(t) \\ &\vdots \\ n_k(t+1) &= P_{k-1} n_{k-1}(t) \end{aligned}$$

For *k* age classes, we have a vector $\mathbf{n}(t)$ of population abundances and we have a $k \times k$ Leslie matrix $\mathbf{A}$.

[12] This is assuming that the interaction coefficients are not symmetric; $\alpha_{ij} \neq \alpha_{ji}$. We are also assuming we can ignore higher-order interactions. That is, for any species *i* and *j*, a_{ij} does not change in value, or minimally in sign, in the presence/absence of a distinct species *k*. If this assumption is false, then things get *much* messier mathematically and the number of parameters to measure becomes much larger. For example, if we must measure all the "triples" a_{ijk} of species and not just their pairwise interactions, then we would have a total of $30 \times 30 \times 30 = 27{,}000$ distinct parameters to measure.

$$\mathbf{n}(t) = \begin{bmatrix} n_1(t) \\ n_2(t) \\ \vdots \\ n_k(t) \end{bmatrix} \quad \mathbf{A} = \begin{bmatrix} F_1 & F_2 & F_3 & \cdots & F_k \\ P_1 & 0 & 0 & \cdots & 0 \\ 0 & P_2 & 0 & \cdots & 0 \\ 0 & 0 & 0 & \ddots & \vdots \\ 0 & 0 & 0 & P_{k-1} & 0 \end{bmatrix}$$

Finally, we have the following population growth equation.

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$$

What is important to note is that how many equations we have in this model crucially depends on the mode of representation. For example, without using matrix algebra, we have *k* distinct equations. However, when we use matrix algebra, we have a single equation of population growth.

In this section, I have argued that the problem of insolubility and interpretation may not be as problematic as Levins suggested. However, I would also suggest that the most serious problem for population biology has always been the ‘‘measurement problem’’. Models laden with many variables and parameters require measurements that are extremely difficult to carry out given the limitations of time, material resources, and biologists.

Conclusion

In this essay, I have provided an analysis of the methodological foundations of Levin’s classic 1996 essay. First, this piece served as a defense of an alternative methodological program that developed from the work of the ‘‘Marlboro Circle’’. Second, it was argued that the essay served as a basis for a critique of systems ecology. Second, Third, Levins’ arguments properly understood are pragmatic; they concern the tradeoffs that occur given our models, the nature of systems studied, and our own empirical limitations. Finally, there are important differences between population biology of 1966 and that of 2005 which suggest that Levins’ strategy of model building may be too pessimistic.

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