

Complex Systems, Trade-Offs, and Theoretical Population Biology: Richard Levin's "Strategy of Model Building in Population Biology" Revisited

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Ecologist Richard Levins argues population biologists must trade-off the generality, realism, and precision of their models since biological systems are complex and our limitations are severe. Steven Orzack and Elliott Sober argue that there are cases where these model properties cannot be varied independently of one another. If this is correct, then Levins's thesis that there is a necessary trade-off between generality, precision, and realism in mathematical models in biology is false. I argue that Orzack and Sober's arguments fail since Levins's thesis concerns the pragmatic features of model building not just the formal properties of models.

1. Introduction. Ecologist Richard Levins (1966, 1968) argues that biologists must choose between building mathematical models that trade-off generality, precision, or realism because of the complexity of biological systems. He also argues that there are several strategies by evolutionists for theoretically coping with complex systems in evolutionary biology and ecology. Levins's claims have not gone unchallenged. Biologist Steven Orzack and philosopher Elliott Sober (1993) attempt to provide a clear account of what generality, precision, and realism are with respect to mathematical models. On the basis of their account, they argue that these model

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desiderata cannot always be traded off in ecology and evolutionary biology.

I present Levins's views on model building in their historical setting and explicate his arguments for the necessary trade-offs therein. I then present Orzack and Sober's analysis of the concepts of generality, precision, and realism, and their counterarguments against Levins's claims. Orzack and Sober argue that given their analysis, there are some cases where these model properties cannot be varied independently of one another. They show that if a model is a limiting case of another model, then the latter is at least as general, precise, and realistic as the former. In those cases where a model is a limiting case of another, then Levins's thesis—that there is a necessary trade-off between generality, precision, and realism in mathematical models in biology—is false. I argue that Orzack and Sober's arguments fail. Levins's thesis concerns the pragmatic features of model building rather than the formal properties of models. The trade-offs are necessary in light of our limitations and not as the result of the semantics of the models themselves.

2. Complex Systems, Models, and Trade-Offs. Theoretical population biology is composed of relatively distinct sciences such as population ecology, population genetics, behavioral ecology, and biogeography. For example, population ecological models typically concern multispecies systems, which are described in terms of their demographics and densities. The environment of the community is allowed to vary over time and, especially in more recent work, space. However, change in gene frequencies, or what is commonly considered evolutionary change, is largely ignored. Likewise, models of population genetics look at the frequency of genotypes in a single species and how they change as the result of natural selection, inbreeding, mutation, migration, and genetic drift. The environment in which a species finds itself is assumed to be relatively unchanging.¹

In the 1960s, ecologist Richard Levins and other biologists such as Richard Lewontin, Robert MacArthur, and E. O. Wilson were concerned with integrating these disparate areas of theoretical biology. At the time, there was increasing evidence that ecological and evolutionary processes are temporally commensurate. For example, significant evolutionary changes in beak size occur seasonally in Darwin's finches as the result of severe draught. Likewise, ecological processes like forest succession can occur over centuries. If ecological and evolutionary processes are temporally commensurate, then these different processes may interact with one another dynamically. One cannot simply separate the "evolutionary play" from the "ecological theatre" in the customary temporal way (Hutchinson

1. Important exceptions are models that represent frequency-dependent selection.

1978). Moreover, if one is concerned with jointly modeling ecological and evolutionary systems, then evolutionists and ecologists must devise models with common state variables and parameters such as fitnesses, intrinsic rates of growth, and carrying capacities. Mathematical modelers must somehow deal with multispecies systems that change demographically and that are evolving in temporally and spatially heterogeneous environments.

A second important concern of Levins was a competing methodological school, systems ecology (Palladino 1990). Levins was explicitly worried with the rise of general ecological models that are designed to be what he calls “photographically exact” (1969, 304). For Levins, the ideas of the ecologist Kenneth Watt, especially in his book *Ecology and Resource Management*, typified this research program. Watt and his coworkers attempted to design universally applicable models that could be simulated on computers and where the only thing that needed to be altered for different systems were the values of the parameters (see Watt 1968, 113). Levins, in his review of Watt’s book, called this method “FORTRAN ecology” (1969, 304).

A “photographically exact” and universally applicable approach to representing ecological and evolutionary systems would consist in writing down a set of equations that contain all of the necessary state variables. Moreover, one must also provide the appropriate parameters including the relevant genotypic fitnesses, interaction coefficients, and other demographic parameters, such as intrinsic rates of growth and carrying capacities. Some of these evolutionary and ecological processes would also involve time lags since their effects are rarely instantaneous. Thus, according to Levins, the model would be an enormous set of coupled partial differential equations with hundreds of parameters. What could one do with such a model? Levins argues that the applications are severely limited.

There are several problems with using such a model. First, the equations would not have any empirical meaning for scientists. The terms of the equations would be in the form of quotients of the sums of products of various parameters. Biologists would have to interpret these equations, which is difficult to do even with relatively simple models (Levins 1968, 5). As an example, consider the amount of conceptual work that has been expended to provide a reasonable interpretation of what the competition coefficient α_{ij} of the Lotka-Volterra interspecific competition model represents. Traditionally, two species are said to compete when each exhibits a negative per capita effect on the other. This leads to reduced abundances or a decrease in fitness or some component of fitness.

There are several worries with this account of interspecific competition, and hence, with what the associated parameter designates. First, this account is extremely phenomenological since there are many different mechanisms of interspecific competition that can generate the negative

pairwise interactions (Schoener 1983). Second, predation by one species on two others can generate *apparent competition* (Holt 1977). If a predator species preys on two resource species in a way that depends on which resource species is most common, then there can exist a pairwise negative per capita effect between the resource species *even when they do not physically interact*. Thus, interpreting a relatively simple parameter is often a difficult affair. If it is difficult to determine the precise meaning of “*x* competes with *y*” and thus interpret the competition coefficient, then consider how much more difficult it would be to interpret a model of coupled partial differential equations with one hundred parameters (Levins 1968, 5).

Second, even if the equations are empirically meaningful to biologists, there are far too many parameters to measure, each of which would require the careers of many scientists to estimate (Levins 1968, 5). In order to see the difficulties, consider a caricature of the work ecologists must perform. Suppose we want to represent the dynamics of an ecological community of twenty species with a Lotka-Volterra multispecies model. We must determine the intrinsic rates of growth and carrying capacities for each of the twenty species. Likewise, we would have to estimate all of the interaction coefficients that would minimally generate a 20×20 matrix describing how each species affects every other species. If the interactions between pairs of species are affected by the other species in the community—there are higher-order effects—then matters would only be made worse since the matrix will become larger. This problem is even more astonishing in light of the fact that most ecological studies are performed over the course of, at most, a decade or two (Pimm 1991). The observational and experimental work to be done to evaluate a “photographically exact” model would be practically impossible to carry out.

Third, even if the first two worries can be resolved, the equations will probably have no analytic solutions. Scientists want more than a model that tells us how a system changes over time. We do not want only to change the system’s variables in small increments of time over and over again with these “evolution equations” to determine what state the system will be in at a future time. Moreover, this incremental investigation of a system ignores important questions concerning the *stability* of those systems. Suppose a system starts in an initial state and at some later time is in some other state. Do other systems that start in states near the initial one also end up near this later state? If the differential equations cannot be solved analytically, then they must be simulated on computers and thus their manageability is crucially dependent on the available technology.

Notice that each of these difficulties is empirical in nature. The complexity of the systems and the resulting limitations of the scientists are determined by the way the world is. The limitations on scientists are of two sorts. First, there are the limitations that arise from our inability to

manipulate and investigate empirical systems as directly as we would like in the field and in the lab. Second, there are limitations in our ability to use our mathematical representations of the systems of interest. Our psychological capacities for storing and retrieving information, carrying out various inferences, and abstracting from details, can make it difficult for us to use certain types of mathematical formalisms for the tasks of interest. Both of these limitations are empirical in nature. Levins (1966, 423) suggests that population biologists have arrived at three strategies (at least) of building models to cope with these complexities and avoid the pitfalls of a “Wattian” approach.

First, one can build a *Type I model* where generality is sacrificed for precision and realism. Levins suggests that some fisheries biologists have offered these sorts of models where the parameters concern the short-term behavior of populations, relatively accurate observations can be made, the equations can be dealt with by computers, and testable predictions relevant to particular situations can be derived (1968, 7). Second, one can build a *Type II model* where realism is sacrificed for generality and precision. Levins suggests that physicists who enter ecology often build models, which are highly idealized, but they hope that the idealizations will result in small deviations from the true equations, will cancel out, or corrections can be made piecemeal (Levins 1968, 7; MacArthur 1972, 33). Third, one can build a *Type III model* where precision is sacrificed for generality and realism. Here one builds graphical models where a functional form is not specified but is assumed to be convex or concave, increasing or decreasing, greater or less than some value, and so forth. The predictions that follow from the model are in the form of inequalities. This is the strategy of model building that Levins himself prefers.

According to Levins, “[t]here is no single, best all-purpose model” (1968, 7). We can continuously improve generality, realism, and precision but only in a pairwise fashion. His argument is composed of essentially two parts.² 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. If the model was of this form, then the equations would be analytically insoluble, uninterpretable, and unmeasurable. If the model was of this form, then clearly the model is of little use to scientists. Therefore, there is an unavoidable trade-off between the generality, precision, and realism of the mathematical models if they are to be of any use to evolutionists and ecologists. Modeling practice in ecology and evolutionary biology does indicate that although the three di-

2. 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). I agree with the former claim but not the latter claim.

mensions cannot be continuously maximized over time, two dimensions can be. If Levins's argument is sound, then it shows the eminent *possibility* of such trade-offs in theoretical population biology and their ultimate *eventuality*. As biologists try to devise increasingly more general, realistic, and precise models, they will eventually arrive at "Levins's impasse." I now want to examine Steven Orzack and Elliott Sober's arguments against Levins's claims.

3. The Semantics of Modeling? To recap, Levins claims that model building in population biology involves a necessary trade-off among modeling desiderata (1993, 533). Since no model of any use can continually maximize all of these properties, we must settle for Type I, Type II, and Type III models. Let us call these claims *Levins's thesis*,

(*LT*) There is a necessary trade-off between the generality, precision, and realism of evolutionary and ecological models such that at most two of these model properties can be maximized per model.

In order to examine this claim, Orzack and Sober rightly argue that the crucial terms of Levins's analysis must be clarified since he does not define them. Orzack and Sober offer the following characterization of the concepts of *generality*, *realism*, and *precision*:

- (*G*) If one model applies to more real-world systems than another, it is more general,
- (*R*) If one model takes account of more independent variables known to have an effect than another model, it is more realistic,
- (*P*) If a model generates point predictions for output parameters, it is precise (1993, 534).

Orzack and Sober also make an important distinction in assessing Levins's claims. A model's parameters and variables can either be *unspecified* or *specified*, where a model is specified if all of its parameters and variables are instantiated with particular values. This distinction is important since an uninstantiated model will always be more general than the instantiated model on Orzack and Sober's account. Hence, we should only compare models that are both instantiated or both uninstantiated.

Orzack and Sober offer several arguments to demonstrate that Levins's thesis (*LT*) is false. Consider their argument that in some cases, generality and realism are necessarily associated. Orzack and Sober utilize the exponential and logistic-growth models from population ecology as examples.

$$dN/dt = rN$$

$$dN/dt = rN(1 - N/K)$$

As $N \rightarrow 0$, the logistic growth equation reduces to the exponential-growth equation. In other words, the exponential model is a *limiting case* of the logistic-growth model as the population size goes to zero. By Orzack and Sober's definitions of generality and realism, the logistic-growth model is more general than the exponential-growth model since any system to which the latter applies, the former applies as well. Moreover, the logistic-growth model is more realistic than the exponential-growth model since the logistic has one more independent variable (or rather the parameter K) which presumably has an effect on the dependent variables. As Orzack and Sober write, "In this case, the two properties are *necessarily* associated; generality and realism are not model attributes that may be altered independently" (1993, 536). More generally, if one model is a limiting case of another model, then the second is more realistic and general than the first is. So, it appears that Levins is incorrect realism and generality cannot always be altered independently.

Orzack and Sober also argue that sometimes realism, generality *and* precision cannot be traded off with respect to one another. Take any precise and uninstantiated model with n independent variables. Suppose we add an $n + 1$ independent variable to the previous model. The second model is more general than the first, since for any system to which the first applies the second must also apply, but not vice versa. The second model is also more realistic by hypothesis, since it has one more independent variable that has a relevant effect on the dependent variables. However, since the first model was assumed to be precise, the second must also be. If the first model generates point predictions, then the second must also. Therefore, there are some models in which generality, realism, and precision can be all maximized simultaneously *and* there can be no trade-offs among them. Hence, (LT) is false.

More generally, Orzack and Sober's argumentative strategy employs the following claim:

For any two models, if the first is a special case of the second, then necessarily the second is at least as general, realistic, and precise as the first.

This claim follows from their (G), (P), and (R) and the fact that one model entails the other under appropriate conditions. If the above thesis is true, then the following thesis must also be true,

(OS) If a model is a special case of another model, then there can be no trade-off between the generality, precision, and realism of the former and the latter.

In this sort of case, one cannot separate the model features as Levins's strategies require. Hence, for some models, there can be no trade-off

between model properties and (*LT*) must be false. If one is to show that Orzack and Sober's counterargument is fallacious, then one must show that (*OS*) and (*LT*) are consistent given the fact that there are nested models in theoretical biology.

4. The Strategy of Model Building Defended. Orzack and Sober surveyed and examined most of the citations of Levin's 1966 paper in the *Science Citation Index* and *Social Sciences Citation Index*. They conclude that "[o]ur impression from this survey is that Levins's arguments have been widely misinterpreted" (1993, 534). I argue below that it is Orzack and Sober who misinterpret Levins's arguments. Levins was not attempting to classify the attributes of models per se, but only insofar as they are relevant to devising strategies for model building. Orzack and Sober argue that in at least some cases there can be no trade-off between the generality, precision, and realism of biological models. Using their recommended definitions, they show that sometimes the three model properties are necessarily connected.

Levins's arguments, however, do not concern that point at all. Even if all three of those properties cannot be varied independently of one another, still there may still be reasons why *we* could not *use* such models where formal trade-offs cannot occur. Levins writes,

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)

Levins claims that there are "contradictory demands" between a complex nature and human minds. Likewise, he claims that there is the "contradictory desiderata" of generality, realism, and precision of mathematical models. Hence, one might think that Levins is claiming some sort of logical inconsistency in maximizing the three model properties. However, this view is in opposition to the very nature of Levins's arguments. He claims that the "contradiction" is the result of the complexity of nature and our attempt to understand that complexity, but nowhere does he claim the conflict concerns models alone.³ Here is Levins again:

3. Importantly, Levins is a Marxist and Marxists often use the term "contradiction" in a much different sense than that of a proposition which is necessarily false (Levins and Lewontin 1985).

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 non-linear partial differential equations, which are usually insoluble, to get answers that are complicated expressions of the parameters which are uninterpretable. (1968, 5)

Thus, Levins argues that the conflict concerns our ability to understand nature. The pragmatic conflicts in model building could be present even if Orzack and Sober are right. If Levins's arguments are correct, then these conflicts can be present even when there are cases where *necessarily* there can be *no* trade-off between generality, precision, and realism.

Let us consider a useful graphical format for representing (*LT*) and (*OS*) (see Levins 1993, 550). Consider a space with the dimensions generality G , realism R , and precision P . Each point in this space represents a model. Thus, we can compare models with respect to how general, realistic, and precise they are. Likewise, suppose that there is a boundary demarcating the set of possible models. I will examine what this boundary represents below. Since it is difficult to visualize a three-dimensional space with a boundary, let us first consider just two dimensions at a time, generality G and realism R (Figure 1). However, nothing of importance hangs on the choice of dimensions since any two of the three will yield the same result.

We want to provide a graphical representation (a meta-model of sorts) in which there is a model that is maximally general and realistic but is such

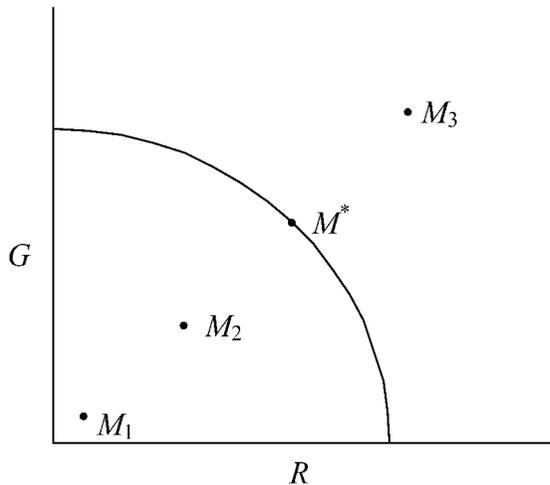


Figure 1. A graphical model of model building with two dimensions, generality and realism

that any increase in either property leads to a decrease in the other. That is, we will suppose that Levins's thesis is reformulated as

(LT^*) There is a necessary trade-off between generality, precision, and realism such that at most *one* of these model properties can be maximized per model.

(LT^*) is distinct from (LT), but examining the former easier case will shed light on the more difficult one. To find such a graphical model that satisfies (LT^*), the shape of the boundary is crucial and must be convex. Suppose there is a model M^* that is maximally general and realistic and is such that there can be no increase in both G and R (though they can be increased separately).

Now consider models M_1 , M_2 , M^* , and M_3 in Figure 1. We can see that M_2 is more general and realistic than M_1 , and there is no trade-off in moving from M_1 to M_2 . Likewise, there is no trade-off in moving from model M_2 to model M^* . However, there is a trade-off at the boundary for M^* . Any increase of G or R along the boundary leads to a decrease on the other axis. This follows from the assumption that the boundary is convex and that M^* is maximally G and R . Now consider the sequence of four models. From Figure 1, we see that as we move from the origin of the space each model becomes successively more general and realistic. Suppose further that M_1 is a special case of M_2 , M_2 is a special case of M^* , and M^* is a special case of M_3 . This sequence of models satisfies the antecedent of Orzack and Sober's (OS). Hence, it follows that there can be no trade-offs between the models in the sequence with respect to their model properties. Granted, this case is different from those that concern Levins since it concerns two model properties at a time. Nonetheless, it appears the above case is inconsistent with (LT^*). So, in order to begin to answer Orzack and Sober in the more complex case let us determine whether (LT^*) is inconsistent with this scenario.

Levins's thesis (LT^*) only concerns those cases where we have a system which is too complex for a mathematical model to usefully represent it in both a general and realistic way. The cognitive limitations of the scientists involved prevent the model from being of any use because it is uninterpretable, unmeasurable, or insoluble. This is what the boundary represents. Hence, the models M_1 and M_2 are irrelevant they are not at the boundary where trade-offs occur. However, M^* is on the boundary and M_3 is outside of it. In our example, there does exist a model M_3 that is necessarily at least as general and realistic as M^* . However, M_3 is *cognitively inaccessible*. By hypothesis, the third model cannot be used by scientists. Hence, any *useful* model above the boundary must trade-off generality or realism. Therefore, there is a "necessary" trade-off between generality and realism. Since this is true of any two of the model properties, then there is a

“necessary” trade-off between model properties. Thus, (*OS*), (*LT**), and the assumption that there are evolutionary and ecological models which are limiting cases of each other are mutually consistent.

This graphical example and (*LT**) concerns only two model properties. However, we can revise the graphical example given so that (*LT*) applies to it. Again, it is difficult to visualize the three-dimensional space with a boundary.⁴ Informally however, it amounts to the following. Suppose we have a three-dimensional space with generality *G*, realism *R*, and precision *P* as the dimensions and that there is a model *M** that is maximally general, precise, and realistic. Now we must think of the boundary as a three-dimensional surface. Essentially, this surface is a “hill” in this space. On this surface, there is a peak where model *M** rests. Let us further suppose that if we increase in any two dimensions from *M**, then there must be a decrease in the third. So, for example, if we increase along *G* and *R*, then we must decrease in *P*. Thus, there is a necessary trade-off between generality, precision, and realism, and at most two of these properties can be increased beyond *M**.

Now consider the argument above concerning the sequence of models *M*₁, *M*₂, *M**, *M*₃. Suppose that we have a space that satisfies the assumptions above. Likewise suppose the sequence of models *M*₁, *M*₂, *M**, *M*₃ is situated in the space as in our previous example and that *M*₁ is a special case of *M*₂, *M*₂ is a special case of *M**, and *M** is a special case of *M*₃. Hence, it follows from these assumptions and (*OS*) that there can be no trade-offs among these models with respect to their generality, precision, and realism. As before, we need only concern ourselves with *M** and *M*₃. *M** is on our surface that represents the “boundary of complexity” and *M*₃ is above it. True enough, we cannot trade off the generality, precision, and realism of *M** as we move to *M*₃; however, *M*₃ is cognitively inaccessible to us. Hence, it cannot be used by us. Likewise, if we are to move from *M** to increase the generality, precision, or realism of a *usable* model, then we can do this for two dimensions at most. Hence, Orzack and Sober’s argument fails with respect to (*LT*).

The fundamental problem with Orzack and Sober’s analysis is that their notion of a “necessary trade-off” concerns the logical or semantical relations between model properties. However, Levins’s notion of a “necessary trade-off” concerns our cognitive limitations and use of mathematical representations and not the logical or semantic properties of models alone.

4. We can define it mathematically in the following way. Suppose that (1) $M = f(G, R, P)$, (2) there is a model *M** which is maximally general, precise, and realistic, and (3) (a) if $\partial f / \partial G|_{M=M^*} > 0$ and $\partial f / \partial R|_{M=M^*} > 0$, then $\partial f / \partial P|_{M=M^*} < 0$, (b) if $\partial f / \partial R|_{M=M^*} > 0$ and $\partial f / \partial P|_{M=M^*} > 0$, then $\partial f / \partial G|_{M=M^*} < 0$, and (c) $\partial f / \partial G|_{M=M^*} > 0$ and $\partial f / \partial P|_{M=M^*} > 0$, then $\partial f / \partial R|_{M=M^*} < 0$.

The boundary in our graphical representations depicts the difference between those models that can be used and those that cannot. Thus, (*OS*) is consistent with (*LT*) even when there are models that are limiting cases of each other. Levins's strategy of model building is left unscathed.

5. Conclusion. I have presented the views of Richard Levins on model building and have defended them against the arguments of Steven Orzack and Elliott Sober. Orzack and Sober misunderstand the nature of Levins's concerns. Levins is interested in the trade-offs that occur as biologists fallibly inquire into extremely complex systems and not in the logical independence of various properties of models themselves. Thus, Orzack and Sober's arguments do not threaten Levins's claims.

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