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The “Structure” of Population Ecology: Philosophical Reflections on Unstructured and Structured Models

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I. Introduction

In 1974, John Maynard Smith wrote in his little book *Models in Ecology*,

A theory of ecology must make statements about ecosystems as a whole, as well as about particular species at particular times, and it must make statements that are true for many species and not just for one... For the discovery of general ideas in ecology, therefore, different kinds of mathematical description, which may be called models, are called for. Whereas a good simulation should include as much detail as possible, a good model should include as little as possible. (1974, 1)

The aspiration of many population ecologists has been to devise minimalist models that describe general ecological patterns. They have worked hard at finding such minimalist models but not without difficulty (of course, there is difficulty in finding general ecological patterns as well). Thus, some recent ecologists argue that population ecology theory should consist less in Maynard Smith's models and more in his simulations. De Roos and Persson (this volume) argue that we must begin again. Since the 1980s, a “paradigm shift” has been occurring. In this essay, I want to consider the rationale of one part of such a revolution and the search of general theory. I consider the case for building structured population ecological models to the near exclusion of unstructured

models as presented by Andre De Roos and Lennart Persson (this volume). First, I sketch what unstructured and structured models are in population ecology. Second, by way of clarifying and strengthening their argument, I contend that the traditional argument for trade-offs between realism, generality, and precision of models is problematic and I sketch what generality means in population ecology. Third, I argue that De Roos and Persson assume an unjustified form of mechanistic individualism and ignore pluralistic model building strategies. Thus, I suggest that they have not made their case for individual-based modeling over the traditional approach.

II. Models, Models, and More Models.

Models in population ecology consist in two types – unstructured and structured. Unstructured models, or what are sometimes called *p*-state models, describe the population with state variables like population abundance or density *N*. In choosing such variables, we make an *identical individuals assumption* – we assume that individuals can be treated as “nearly” identical. That is, we suppose that when they differ little is lost by aggregation or averaging over those differences. Most of traditional theoretical population ecology consists in *p*-state models.

Structured models, or *i*-state models, come in one of two types. In *individual distribution models*, we relax the assumption of identical individuals. One represents differences among individuals through placing them in different classes with respect to age, sex, or size for example. Of course, by grouping individuals by age, sex, or size, we are assuming that the individuals are identical

within each class. This is an idealization though one which is less capricious than the identical individuals assumption. In *individual configuration models*, one represents each individual of the population and tracks their changes through simulating their behavior computationally. Hence, in individual configuration models we find no reminisce of the identical individual assumption.

As noted above, traditional population ecology consisted in largely unstructured population models as Hastings (this volume) masterfully describes. This classic theory includes density-independent and density-dependent population growth, interspecific competition, predatory-prey, epidemic, and host-parasitoid models (see Hastings 1997). As one example of such models, consider the Lotka-Volterra predator-prey model. To derive the model, let us make the following assumptions:

- Growth of prey population is exponential in absence of predators;
- Predator declines exponentially in absence of prey;
- Individual predators can consume an infinite number of prey;
- Predator and prey encounter one another randomly in a homogenous environment;
- Individuals in the predator and prey populations respectively are ecologically and genetically identical;

So, if we let r represent the intrinsic growth rate of the prey, a represent the capture efficiency of the predator, b represent the conversion efficiency of the predator, and q represent the mortality rate of the predator, then have the following model where V is the prey population and P is the prey population.

$$\frac{dV}{dt} = rV - aVP$$
$$\frac{dP}{dt} = baVP - qP$$

In effect, we have used a “law of mass action” in deriving the model. The interactions between predator and prey are proportional to their respective abundance. However, ecologists know that encounters between predator and prey are non-random and individuals are not identical. Much ink has been spilt in attempting to deal with the first assumption. The Lotka-Volterra model above was modified so that the prey grows logistically and the predator is satiated. Now there are lots of models that incorporate spatial heterogeneity; the most recent being metapopulation models and spatially explicit models involving diffusion equations (Tilman and Kareiva 1997). However, the assumption of identical individuals has largely been ignored.

There are two important anomalies for models including this assumption. First, ecologists know that individuals are not identical in their ecological and genetic properties. Moreover, those properties change through time. As Darwin noted, and proponents of structured models remind us, variation is the rule not the exception. Thus, the identical-individuals assumption is patently and obviously false. However, we are accustomed to idealizations in models so the question is whether this falsehood makes a difference and this takes us to the next problem. Second, the bulk of predator-prey theory predicts predator-prey cycles and these cycles are according to De Roos and Persson rarely found in nature or at least outside the lab (this volume, 5-6). This is just a special case of the fact that unstructured models have not been terribly successful empirically

according to the critics. So, why not relax this assumption of identical individuals? De Roos and Persson suggest that we do just that. Given the fact that the identical individual assumption is false and that the models based on it are empirically deficient, they argue that we need to reorient model building in population ecology.

As an example of an individual distribution model, consider the following simple density-independent population growth model. Let $n_i(t)$ represent the number of individuals at time t in age class i . Suppose there are k age classes in the population. Thus, the age structure at time t consists in the following vector of abundances.

$$\mathbf{n}(t) = \begin{bmatrix} n_1(t) \\ n_2(t) \\ \vdots \\ n_k(t) \end{bmatrix}$$

Using information from fertility and survivorship schedules from traditional life table analysis, we can predict how the age structure changes from $\mathbf{n}(t)$ to $\mathbf{n}(t+1)$. Let P_i be the probability that an individual in age class i survives to age $i+1$. Similarly, let F_i represent the average number of offspring produced by an individual of age class i . For example, if our population has k age classes, then we have:

$$\begin{aligned} n_1(t+1) &= F_1 n_1(t) + F_2 n_2(t) + \dots + F_k n_k(t) \\ n_2(t+1) &= P_1 n_1(t) \\ n_3(t+1) &= P_2 n_2(t) \\ &\vdots \\ n_k(t+1) &= P_{k-1} n_{k-1}(t) \end{aligned}$$

Thus, for k age classes, then we have a $k \times k$ Leslie matrix.

$$\mathbf{A} = \begin{bmatrix} F_1 & F_2 & F_3 & \cdots & F_k \\ P_1 & 0 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 & 0 \\ 0 & 0 & \ddots & 0 & 0 \\ 0 & 0 & 0 & P_{k-1} & 0 \end{bmatrix}$$

Finally, we have the following population growth equation.

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

It is very difficult to provide an example of an individual configuration model given that they are often written in code in a programming language of choice so I will not attempt to present such a model. However, individual distribution models consist in either matrix models, delay-differential equations where the classes are discrete and time is continuous or partial differential equations where both are continuous (Caswell et. al. 1996, 4-8).

De Roos and Persson suggest that modeling in ecology should consist in several stages (this volume, 6):

- Determine the dynamical patterns of the system of interest,
- Determine which features of these dynamics are generic—what form general patterns, and
- Identify what mechanisms are responsible for those patterns.

Supposing that such general patterns exist and can be identified, they suggest that the mechanisms generating such patterns reside at the level of individual interaction and behavior. For De Roos and Persson, this provides an account of the structure of modeling strategies. Instead of beginning with “top-down” unstructured models, one should begin with “bottom-up” structured models.

These unstructured models are not then “complexified” by adding more realistic assumptions, but are limiting cases of the structured models when individual variation is low or interactions between individuals are approximately random.

They write,

In our view general theory can only be derived if we understand what is lost or neglected by not including specific aspects or mechanisms into a model. In other words, generality can only be achieved by selectively deleting details from more complex, mechanistic bottom-up models, as opposed to a priori deciding on what the essence of a system is and refraining to include any mechanism at all for the sake of being too specific. (this volume, 7)

Put a different way, we begin with a “richly mechanistic” structured model “...and successfully simplifying it until it fails to produce realistic dynamics” (Judson 1994, 12).

In the remainder of this essay, I want to examine the case for structured population models. I will first try to clear some of the brush in favor of their defense. This requires returning the issue of trade-offs in model building since many ecologists still believe that there is a necessary trade-off between realism, generality, and precision (see Hastings (this volume, 16) as an example). Put differently, one must choose between “strategic” and “tactical” models. This potentially begets problems for structured population models since they purport to realistic, general, and precise. I will argue that things look brighter than they did when Richard Levins first argued for this claim in 1966. Likewise, we need to be clearer about what “generality” is and what makes a model general. There is a prejudice against structured models since it is believed that they are less general than unstructured models and once we are clearer as to what *generality* is we this is not so. However, there are two points that I believe count against De Roos and

Persson's case. In effect, they make the assumption that general population-level patterns are generated by individual mechanisms and not population-level mechanisms. This of course may be true but they need an argument for this claim. Second, in assuming that we start with structured models and only move to unstructured models later, they ignore pluralistic model building strategy which investigates both unstructured, individual distribution, and individual configuration models. I claim it retains the strength of their own proposal and avoids its weaknesses (see Hastings (this volume) as well).

III. Revisiting Modeling Trade-Offs.

In 1966, Richard Levins argued that there is a necessary trade-off between the generality, precision, and realism of ecological and evolutionary models. Ultimately, two of these model properties alone can be maximized per model. These necessary trade-offs are due to the psychological and computational constraints of modelers and the complexity of the systems of interest. An optimally general, precise, and realistic model would require a very large number of parameters in a very large number of coupled partial differential equations. A model of this form would be analytically insoluble and the terms of the equations would be unmeasurable and uninterpretable. Obviously, the model would be of no use to scientists. So, there is an inescapable trade-off between the generality, precision, and realism of the mathematical models if they are to be of any use to ecologists and evolutionists (see Orzack and Sober (1993), Levins (1993), and Odenbaugh (2004) for a recent discussion).

Levins own solution to this problem was to suggest modelers maximize two model dimensions at a time giving his famous trichotomy of Type I, Type II, and Type III models. We can devise models that are general and realistic but sacrifice precision, or devise models that are general and precise but are not realistic, or devise models that are general and realistic but not precise. His predilections leaned toward type III models. However, he was a pluralist recognizing that different strategies yielded different fruit. As historian of population ecology Sharon Kingsland writes,

Levins was arguing here not only for the place of modeling in population biology as the only way to cope with complexity, but for the need to foster a pluralistic style of ecology to piece together a general theory of community structure from many sides. Of course he realized that the choice of different models or strategies would reflect conflicting goals and even conflicting aesthetic standards on the parts of biologists. For this reason he regarded disagreements about methods as basically irreconcilable. But he saw the alternative approaches, even of opposing schools, as partaking of a larger “mixed strategy” which would fit different pieces of the puzzle of community structure into a coherent whole (1995, 190).

On his view, theories in population biology consist in “families of models”. Models should be articulated on the basis of each of the strategies removing the deficiencies of the others. Though I will explore this notion of a “mixed strategy” in section 6, I think there is room for resisting his conclusion that there is a necessary trade-off. The limitations of 1966 are not the limitations of 2004.

First, it does not follow from the fact that ecological models have no closed form solutions that the models will be useless. It is well known in physics, chemistry, *and* biology that many models do not have analytically tractable solutions. However, this does not mean that we cannot use these differential or difference equations. Rather, it is our computational abilities that must be

augmented. The most successful way of doing this is through using computer-based numerical techniques (see Humphreys 2004 for discussion of computational science). In effect, we are *inductively* exploring the behavior of models for a wide variety of variable and parameter values. We can then find regularities or patterns in the model's behavior. This in fact is exactly the sort of analysis that Caswell et. al. (1997, 10-13) recommends. In simulating structured models computationally, we must determine the asymptotic behavior, transient behavior, and perform a perturbation analysis.

Of course, it would be unfair to blame Levins for overlooking these methods given that they were not available to biologists in 1966. These computational methods are all the more important given that many of the obstacles facing structured models and individual-based models are computational limitations.

Second, I would agree with Levins that if a model is so complex as to be uninterpretable, then it will be useless. However, I would deny that the equations in population biology need be this complex. Levins would have us imagine a model with an enormous number of variables and parameters. We should notice though that the individual distribution models under consideration do not have a large number of distinct variables and parameters *types*. Even if these models consist in a large number of equations we certainly would know what the equations *mean*. This is even more apparent given that the number of equations crucially depends on the mathematical formalism we choose. In matrix algebra, we reduced k equations to single equation in our age-structure model above. This objection has more force when we consider individual configuration models.

There we have parameters which represent each individual and their properties. However, if we can summarize this information informally or formally, then it is possible to at least describe the assumptions of the models. Nonetheless, I am sure “non-transparency” of these models is one of the reasons that ecologists have been skeptical of individual-based models. Hence, I would claim that the problem of interpretation is manageable contrary to Levins’ argument.

Hastings writes,

As emphasized in a variety of classic papers discussing models in ecology, models are useful because they are simplifications. In any use of models in ecology or population biology, there is an important tradeoff between simplicity and biological realism (Levins, 1966). The advantages of biological realism that are incorporated into structured models may be offset by difficulties in matching up to data and proliferation of parameters, as well as complications precluding complete analysis. An important conclusion is that the continuing in the tradition started by Lotka and Volterra is not a dead end. (this volume, 16)

If there is a problem that makes “mechanistically rich” mathematical models extremely difficult to utilize in ecology, it is the fact that the sheer number of variables and parameters that very difficult to measure and estimate in natural systems. As we increase the realism of our models, then the number of variables and parameters increases. Our models must be relatively system-specific or phenomenological if our laboratory and field studies are as limited as Levins and Hastings would have us believe. This is what I believe to be the chief difficulty for structured and individual-based models.

IV. Generality?

Ecologists love a general, testable theory. They are those who doubt the very possibility of such a thing (Dunham et. al. 1999). However, many important

ecologists have claimed that science requires it so we had better find it. Most famously, Robert MacArthur wrote,

To do science is to search for general patterns. Not all naturalists want to do science; many take refuge in nature's complexity in a justification to oppose any search for patterns. This book is addressed to those who do wish to do science. (1972, 1)

However, it is crucial to souse out exactly what a "general" theory or models consists in.

There are several ways in which a model can be general. Better yet, 'generality' is a comparative term; hence, there are several ways in which a model can be more general than another model. First, here is a common definition implicitly used by ecologists:

A model is more general than another model just in case the former applies to more systems than the latter (see Orzack and Sober (1993) for similar proposal).

Clearly, from a philosopher's point of view, this will not do since we must more carefully determine what 'applies' means here. There are two ways in which we can flesh out this notion of application.

A model is more general than another model just in case the former *represents* a larger number of systems than the latter.

A model is more general than another model just in case the former *successfully represents* a larger number of systems than the latter.

There are two ways of construing "large number of systems". If we simply mean that one model represents a larger number of specific populations than another model, then we are simply tallying individual populations. However, this is not the only interpretation available. Consider consumer-resource models and host-parasitoid systems. Every host-parasitoid system is a consumer-system but not

vice-versa. Thus, “larger number of systems” can also be construed as “larger number of system types”. Ideally, general models would accomplish both but it is important to note the difference.

To determine what a model represents we scout for the dependent variables. If the dependent variables are host population H and parasitoid population P , then the model represents host and parasitoid populations given our usual conventions. If the dependent variables are consumer population C and resource population R , then the model represents consumer and resource populations given our conventions. However, it is one thing to represent some system and it is another to successfully represent the population. To successfully represent a system I mean nothing more than that *either* the assumptions of the model are “approximately true” *or* the model’s dynamics bear a sufficient goodness-of-fit to the population via a time series or some other data set. Assumptions of models include the functional form of the equations, the number and type of variables, and the number and type of parameters. Statistical model selection criteria such as the Akaike and Bayesian Information Criteria allow us to evaluate models based on their assumptions *and* fit to data (see Mikkelsen [2003, forthcoming] for interesting discussion of AIC in ecology). I believe that ecologists are most interested in successful representation, and thus are most interested in generality as characterized in the last form.

What is absolutely important to recognize is that what variables or parameters one chooses has little to do with generating general models in the aforementioned sense. The fact that abundance N includes individual organisms does not guarantee that an unstructured model will be more general than a

structured model. It all depends on how successfully the model represents the phenomena of interest. To suppose that a model with more general variables (dependent variables represents broader system-types) will be a more successful representation than a model with less general variables (dependent variables represents less-broad system-types) is just to assume a priori what surely must be determined a posteriori. Moreover, De Roos and Persson argue that the evidence suggests that just the opposite though I have not argued that here. By being careful about the sense of 'generality' one uses, we can at least clear the way for a defense of structured population models.

V. Reductionism Redux

Now I want to turn to worries I have about De Roos and Persson's proposal. They explicitly assume that the mechanisms that generate population patterns occur at the level of individuals. They write,

This sequence of steps [their modeling strategy] necessitates that the modeling of the population or community of interest starts out at the level, at which the dynamics originates: the level of individual organisms. (this volume, 6)

From their point of view, individuals are born, die, migrate, develop, feed, forage, and reproduce after all and *these* are the processes that determine populations rates. *However*, De Roos and Persson simply ignore the possibility that there are population-level mechanisms that drive population change. There is a popular metaphysical account of levels of organization that agrees with De Roos and Persson that individual mechanisms give rise to population rates but also

countenances population-level mechanisms. It is that account that I want to sketch here.

Philosophers are familiar with the idea of “multiple realization”. A higher-level property is multiply realizable just in case it can be realized by more than one lower-level property. An ecological example of such a functional property is that of a Simpson’s species diversity or $\sum_i \log p_i n_i$. It is a property of communities and is determined by the species richness and the relative abundance of those species. However — and this is the salient point — two communities can have the same Simpson diversity index but yet have different relative abundances or different species richness (see Levins’ similar notion of a “sufficient parameter” [1968, 6-7]).

One should also note that this does not mean that multiply realizable properties are “emergent” in some dubious sense. Given an appropriate set of lower-level properties, the higher-level property is determined. Philosophers often couple the notion of multiple realization with the concept of *supervenience*. One way characterizing supervenience is the following: a family of properties Q : $\{Q_1, Q_2, \dots, Q_n\}$ supervenes on a family of properties P : $\{P_1, P_2, \dots, P_n\}$ if, and only if, for any two objects that have exactly the same P properties must also have exactly the same Q properties; however, the converse does not hold. It is in virtue of these multiply realizable properties that there can be generalizations over populations that cannot be explained simply by considering the individuals of the population. If there are population-level multiply-realizable properties and those properties are causally related to other such properties, then there can be general

population patterns generated at the population level and explained by that level's dynamics. Thus, it would a mistake to simply assume that all of the mechanistic work is occurring at the individual level.

Of course, whether there are such broad, multiply-realizable properties is an empirical issue and I have not defended that possibility. To put this in a less metaphysical way, whether there are general population patterns that can be causally explained by population-level generalizations depends on whether such population-level generalizations exist. It surely may turn out that the contingencies of history and complexity (Sterelny 2001; Odenbaugh 2004) render any such generalizations false. However, there has been a resurgence of the view of ecological laws (Ginsberg and Colyvan [2004] and Mikkelson [2004]). Robert MacArthur, an admirer of general patterns if there ever was one, was ironically very sympathetic to such a position. He argued that there may be no population-level general patterns or mechanisms; rather, the general patterns and mechanisms occur at the level of the community.

The question is not whether such communities exist but whether they exhibit interesting patterns about which we can make generalizations. This need not imply that communities are superorganisms or have properties not contained in the component parts and their interactions. Rather it implies simply that we see patterns of communities and that, at this stage of ecology, the patterns may be more easily related than the complex dynamics of the component species. There is nothing mysterious about this: the relations between the temperature, pressure, and volume of a gas were made into "laws" long before their molecular interpretation was known, and Mendel's laws were clear before his inferred genes attached to the visible chromosome. (1971, 190)

Let me close this section with two implications of this discussion. First, if there are no multiply realizable properties at the population-level, then this means that there will be no *general* population-level patterns. Thus, there will be

no bottom-up explanations of such patterns. Even if there are multiply-realizable population-level properties, it doesn't follow that there are causal relations between such properties. After all, the general population-level patterns could be epiphenomena of the mechanisms governing the individuals. Therefore, it doesn't follow that if there are general population-level patterns, there are population-level mechanisms. This leads to my final criticism.

VI. Structural Pluralism.

De Roos and Persson argue that we should begin with bottom-up models and only try to devise top-down models when we have evidence that the identical individual assumption is roughly correct when encounters are approximately random. They claim that the top-down approach has been assumed a priori. We can understand this criticism in one of two ways. First, we can see those early theoreticians as believing that unstructured models *must* succeed independent of those models having been tested. One might have believed this on the basis of analogies with the success of physics and chemistry in making similar assumptions with the theory of gases and chemical reactions. Interestingly, Huston, DeAngelis, and Post argue that laws of mass action do not always work in physics either. They claim that phenomena like the “spontaneous onset of ferromagnetism near critical temperature, the condensation of water vapor into liquid droplets, and the development of galactic structure” (1988, 683) as being due to strong local interactions and not susceptible to identical individual assumptions. On the other hand, one might have believed that unstructured models *might* succeed and there are no other available types of models that can

be offered which can fulfill the goals at hand. Imagine you are Vito Volterra or Alfred Lotka. You devise the simplest models you can and hope that nature cooperates. This was not only a *plausible* place to start but given the computational limitations that existed it was the *only* place to start. Thus, De Roos and Persson write, “This sequence of steps contrasts strongly with the approach, currently in vogue, in which the ‘essence’ of a particular system is *a priori* decided upon and invariably includes only population-level aspects” (this volume, 7). I think this would not be an apt criticism of Lotka and Volterra.

I suggest that the latter is the most charitable way of reading the history of these early efforts and thus I think this was imminently reasonable for Volterra and Lotka to have done. Nonetheless, given that those limitations have been pushed back at least to some degree, then we can now pursue bottom-up models.

However, should we not pursue *both* strategies at once? That is, given some phenomenon we want to understand or anticipate why can we not allocate theoretical resources amongst unstructured, structured, and individual-based models? Why should we choose one of these model types as the “null strategy”? Hastings agrees when he writes,

Despite the obvious need for and importance of structured models in ecology, unstructured models focusing only on population sizes and ignoring space have not only played an important role in ecology, but they clearly will continue to do. (this volume, 16)

This “mixed strategy” in its simplest form would be to apportion theoretical resources between each model-type equally. I suspect the reason why we should not do this is that the unstructured models have been tried time and again. We are less likely to garnish radically new insights with unstructured models than

with the structured models. However, as Hastings argues, given the new tools of model selection, we can test our unstructured models in very powerful ways.

Consider a literal science fiction (see Kitcher 1993, Strevens 2003). Suppose that the probability of success in explaining general population patterns is a function of effort with diminishing returns. One can think of effort consisting in the number of hours devoted to a model type or the number of researchers working on a model type per unit time. In effect, the reward per unit effort in exploring unstructured models has flattened and we are at the steepest part of the reward curve with respect to the latter two types of models. Thus, we maximize our change of success by apportioning more effort with respect to the latter model types than the former. This I find to be a plausible argument; however, we should never put all of our eggs in one basket. Hence, the most efficient strategy it seems would be to pursue the structured models but to continue work on the unstructured models.

In effect, I am recommending a “mixed strategy” that I believe is precisely what Levins had in mind. What is crucial is that we integrate these models types in our attempt to understand what ecological patterns we can discern.

VII. Conclusion

In this essay, I have attempted to defuse the charge that structured models are problematic because they are realistic, general, and precise and I have also attempted to clarify the nature of generality that population ecologists pursue. Nonetheless, it appears that De Roos and Persson have not yet made their case for a mechanistic, individual-based modeling strategy. Their preferred strategy

contains an unwarranted (or at least undefended) mechanistic individualism and they have ignored a plausible pluralistic, “mixed” strategy combining unstructured and structured models. Thus, I contend that the best “structure” for theoretical population ecology is still left open.

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