The Explanatory Tools of Theoretical Population Biology

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1. Introduction

There is, at present, controversy surrounding the role of the mathematical models which typify the more theoretical portions of ecology and evolutionary biology. Within these sciences there has been controversy about the "testability" of these models, both in terms of the ability of the model to make precise enough claims about the world, and in terms of our ability to determine the values of theoretical parameters. There has been concern, particularly in ecology, about the lack of realism characteristic of most models as well. These are, for the most part, issues involving the nature of theoretical explanation. Much of the current debate about null hypothesis testing, the unfalsifiability of theory, and the role of theory is symptomatic, it would seem, of the fact that these sciences have not settled on what to expect from their most mathematical theories. If there is one emerging theme, it is the need, again especially in ecology, for pluralistic theoretical treatments - which suggests that they may have been expecting too much.

The call for pluralistic theoretical treatment suggests a lack of confidence in laws. Is it because the models *are* just models that we need so many of them? Jonathan Roughgarden says "It is difficult to imagine what could ever qualify as a "law" in ecology. Ecological theory is no more than a collection of tools." (Roughgarden 1984, p.17). This raises a number of challenging questions. If good theories do not at least approximate laws of nature, then what makes a good theory explanatory? What is it for a theory to function as a tool? What is it for one tool to be better than another?

Not having answers to these questions has generated controversy in the philosophy of biology. I have argued elsewhere that disagreements about the nature of theoretical explanation in ecology and evolutionary biology lie at the heart of a triangular controversy over the foundations of the theory of natural selection.[1] In brief, the situation is as follows. Theoretical explanation which involves what we might call radically supervenient properties can, it seems, be explanatory, but it is not exactly clear how. By a radically supervenient property I mean a supervenient property whose basis - the circumstances upon which it supervenes - is (relatively) unsystematizable except in terms of the supervenient property itself. Fitness is an example; it is a familiar point by now

that there is little one can systematically say about the supervenience bases of fitness measures. The question then is how this kind of theory can be explanatory? Is it still a kind of causal explanation, in spite of the radical supervenience? Is it some kind of functional explanation that works in terms of non-physical laws?[2] Is it evidence that explanation needn't function in terms of laws? If so, how might that come about? Not surprisingly, these questions mirror the questions at the end of the previous paragraph.

Both sets of issues - understanding the controversy over the role of theory in ecology and evolutionary biology, and clarifying the nature of theoretical explanation in these fields - are obviously extensive. Furthermore, there is a sense in which both must be pursued at the same time. In what follows I will be attempting primarily to clarify the problems by looking at some examples of the application of supervenient theory, and what some of the biologists have to say about it, with an eye toward gaining a measure of focus on the philosophical problem surrounding the explanatory potential of such theories.

2. Community Ecology: Theories as Tools

A recurring theme among community ecologists these days is the pluralistic nature of ecology. Ecologists must use a variety of different methodologies because ecological questions tend to have complicated answers. In particular, there are few questions whose answers do not depend a great deal on the details of the situation, details such as the kinds of organisms involved, the nature of the environment, and the vagaries of history. As the questions and the details vary, the methodological approaches suited for the task also change. This methodological pluralism goes hand in hand with a pluralistic approach to theory. Diamond and Case draw what seems an appropriate analogy.

> Suppose for comparison that the genetic code, instead of being determined solely by DNA, was codetermined by seven classes of macromolecules, whose relative role in a given species varied with age, season, weather conditions, and time since the last glaciation and also tended to differ between large and small species, ectotherms and endotherms, and herbivores and carnivores. If this were true, we would surely not have our present complete understanding of the code. Yet this is exactly the problem that ecologists face in trying to understand how species abundances are codetermined by competition, predation, herbivory, disease, parasitism, mutualism, and weather. The answers to general ecological questions are rarely universal laws like those of physics. (Diamond and Case, p.x)

In short, the belief in a need for a plurality of theoretical approaches seems to be grounded, at least in part, in a scepticism regarding the existence of fundamental and comprehensive laws governing ecological reality.[3]

As Roughgarden's comment about theories as tools suggests, doubts about the existence of fundamental laws tends to foster an instrumental attitude toward theory. But this instrumentalism is not what philosophers typically associate with the term. Instrumentalism is usually an elaboration of the thesis that in some sense or other the cognitive virtue of theory lies in its ability to save the phenomena, to function as a predictive device. The theoreticians in community ecology would be ill-advised to rest the merit of their efforts on such foundations. Ecology in general is not a very predictive science, and community ecology is one of the more difficult areas in which to forecast the future. Stephen Stearns, for example, claims:

> In community ecology, both predictions and assumptions of most models have been shown to be false. While virtually everything we know that is reliable has

been established through experiment, it is also true that numerous experiments would not have been done had not some theory framed a hypothesis more precisely, or placed it in a more general context, than had been done before. (Stearns 1982, p.639)

In what sense then are theories instrumentally valuable? If they are not primarily *predictive* tools then what kind of tools are they? At least part of the answer is itself suggested by the latter part of Stearns' remark; the virtue of theory lies in its ability to structure the problems of community ecology, to supply good ways to think about these problems. The instrumental virtue of such theories is not (primarily) their predictive utility, but their utility in the search for particular explanations. Can we gain a clearer picture of what this virtue is like? We begin the investigation with an allied discipline which in many ways parallels the development of theoretical ecology.

3. The Use and Abuse of Theory in Population Genetics

In an interesting paper on the role of theory in population genetics, Richard Lewontin provides the following interpretation.

The first point is that population genetic theory is not designed to choose among competing causal hypotheses....Rather, population genetic theory is a descriptive theory that provides the mapping of causal processes as genetic outcomes. It says, '*if* mutation rates are such and such, *if* the mating pattern is such a one, *if* there are five genes affecting the character with the following norms of reaction, *then* the trajectory of the population in time, or the equilibrium state, or the steady state distribution of gene frequencies will be such and such'. (Lewontin 1985, p.10)

On the face of it, the conditional nature of the theory should not preclude the possibility that the theory can be used to choose between competing causal hypotheses. Presumably, the causal regularities of the world are themselves conditional in nature, yet knowing the regularities involved would be just the ticket for making such choices. At least that would be the case if we also knew when we had an instantiation of the antecedent of the law. Lewontin's point is that in population genetics we are almost never in such a position. The parameters of population genetic theory represent very complex causal stories; in the vast majority of cases that story is simply out of epistemic reach. Lewontin lists the following problems.

First, it is very difficult to measure the actual rates of mutation and migration, the actual patterns of mating relations, actual $l(x)$ and $m(x)$ schedules of phenotypes, and norms of reaction of the various genotypes, even if the genotypes could be identified. Second, the genotypes cannot always be recognized, especially for metric characters. Third, developmental patterns, probabilities of survival and reproduction, and behavioral phenomena like mating and migration, are all contingent on a variable environment, and they cannot be measured once and for all....Fourth, in the case of deducing the past from the present, we would need to know the past environments, an impossible task. (Lewontin 1985, p.6-7)

The upshot of this epistemic predicament is that the theory will not function very well as an inference ticket in good old H-D fashion. The data we can get are likely to be consistent with a number of alternative causal hypotheses. This, I take it, is what Lewontin means when he says that theory cannot choose between competing causal hypotheses.

One of Lewontin's responses to this situation is to point out that theory must be understood as playing a different role. The theory does not isolate the actual causal story,

but it does constrain the class of potential candidates. The causal hypotheses under consideration must all be consistent with the theory (unless one is prepared to abandon or modify the theory). As an example, he cites the fact that any hypothesis involving the change in frequency of a trait as a result of selection presupposes (from the standpoint of theory) that there is heritable variation in the trait. It may be impossible to actually determine whether the trait changed as a result of selection or of drift strictly in terms of further application of the theory because it may not be possible to obtain the kinds of parameter values that would be necessary for the discrimination. In such a situation a more direct approach to the mechanism must be found. As he puts the matter:

> The delineation of the prohibited and the possible is the function of population genetic theory. The revelation of the actual is the task of population genetic experiments, a task that such experiments can accomplish provided they are freed of their strong dependence on the quantitative and statistical relations predicted by theoretical formulations and instead are constructed to provide unambiguous qualitative information. (Lewontin 1985, p.11).

In addition to the need for a greater appreciation for the role of experimentation, there is a second moral which Lewontin draws from this interpretation of theory. He argues that there is a current tendency in population genetics to invert the role of theory. Rather than fixing the bounds of the explanatorily acceptable, theory is being used to infer values of the parameters which cannot be measured. Thus, for example, one might attempt to infer genotypic fitnesses from genotypic frequencies in successive generations based on the theoretical relationship between fitness and frequency change. But, as Lewontin points out, Prout (1965) has shown that "...*in principle* no procedure involving the genotypic frequencies in two successive generations will yield correct fitness estimates." (Lewontin 1985, p.7, see also Lewontin 1974, pp.238-239). Thus, the second moral goes hand in hand with the first; with a recognition of the limitations of theory as a means to literal truth, attention can be turned to designing experiments that will provide the "unambiguous qualitative information" necessary for selection among competing causal hypotheses.

Lewontin's points carry over with remarkable fidelity to ecological theory. As the passage from Diamond and Case suggests, the same kind of causal complexity that plagues the population geneticist also exists among the determinants of community structure. In fact, the situation is in some ways worse. Ecological theory, unlike population genetics, does not possess a unitary theoretical structure in which all relevant forces can be embedded. One finds competition theory, predation theory, optimal foraging theory, etc., and one also finds efforts to put pairs of these together, but in general there is no overall theoretical structure in which to consider an array of forces acting in concert (see Schoener 1986 for a discussion of what such a theory might look like). Furthermore, this causal complexity makes it necessary to treat theories as giving the kind of conditional advice that Lewontin discusses. The theory says what will happen over a certain range of parameter values, but it does so only given the satisfaction of an unwieldy *ceteris paribus* clause. There are a number of ways a theoretical inversion like the one Lewontin discusses can go awry. To begin with, there are determinants which have been given theoretical treatment, but not by the theory in use. The success of the inference rests on the insignificance of these forces. In addition, there are forces ecologists are only now beginning to consider, such as ontogenic niche shifts (Werner 1986) and indirect effects (Wilson 1986). Again, the *ceteris paribus* clause must postulate their irrelevance. Thus ecologists often emphasize the same kind of conditional role for theory which Lewontin attributes to population genetics. (Diamond and Case 1986, Roughgarden 1983, 1986, Peter Abrams, personal communication).

If Lewontin's remarks are to be a guide, then we have taken a small step toward answering our original question about the role of theory. We have moved from Stearn's claim that theory functions as a way to structure problems to the slightly more precise idea that theory "delineates the prohibited and the possible". In what way does theory perform this modal function?

4. Theories and Modal Information

We can use an idea introduced by Peter Railton (1981) - the ideal explanatory text - to get a handle on this question. The ideal explanatory text for a given event is, in effect, the causal history leading up to that event. I have discussed the idea in more detail elsewhere (Cooper 1988, 1989); here I will simply assume that the idea of a complete causal history is unproblematic.[4]

How can Lewontin's idea be expressed in terms of this framework? The interpretation of the possibilities is straightforward; they are possible ideal explanatory texts and portions thereof. That is, they are the *causal* possibilities. But it is not as clear how the theory manages to provide these possibilities. There *is* an obvious sense in which state-space theories determine possibilities; the laws of transformation supply the possible trajectories of the system relative to a given initial state. Of course, if the theory is to be any good there had better be some congruence between what it says is possible and what is actually possible. Since the latter is given by the actual laws of nature, one way for a theory to be virtuous on this score would be to express (or at least approximate) the true laws. One of the standard defenses of scientific realism has been that this is the only (or at least the best) way to explain the fact that our theories have had the predictive and explanatory success they have had (see for example Boyd 1973). But this is only a good explanation if, in fact, such causal laws exist. What if there are no actual laws at the level of generality at which our theoretical laws of transformation are pitched? If there are no such general truths for our theories to capture, does that mean that these theoretical efforts have no explanatory merit? I have argued elsewhere (Cooper 1989) that there are certain basic contingent questions whose answers ought not be presupposed by one's account of explanation. The existence and scope of genuine indeterminism is one such question. Likewise, it seems to me a mistake to base explanation on a contingent assumption about the ultimate simplicity of the causal structure of the world. But such an assumption is just what tying the explanatory virtue of theories to the actual laws involves.

There is another reason for holding open the possibility that a theory can be explanatory without actually approximating causal regularities. Theories constructed in terms of radically supervenient properties apparently play just such a role. There is a sense in which heterozygote superiority explains the balanced polymorphism associated with the sickle-cell case, but there would seem to be no place for fitness attributions in the ideal explanatory text associated with this phenomena. Given the causal details, fitness attributions become otiose (see Rosenberg 1983, Cooper 1989 for an elaboration of the argument). The theory expressed in terms of the supervenient property of fitness provides a kind of explanatory information, and if Lewontin is right, it does so by providing modal information, but it does not give us a portion of the actual ideal text - it does not actually make reference to the causal mechanisms and processes responsible for the phenomena. How does such a theory provide explanatory information?

Railton mentions several ways in which explanatory information may be provided. Most relevant for our purposes is his discussion of statistical mechanics. He interprets the statistical manipulations involved in the following way:

> Briefly, ... such appeals to combinatorics serve to illuminate a significant feature
> of the causal processes underlying the behavior of classical thermodynamic sys-
> tems, thereby serving to illuminate the relevant ideal explanatory text in particu-
> lar cases....This illuminates a *modal* feature of the relevant ideal explanatory
> texts: this sort of causal process is such that its macroscopic outcomes are re-
> markably insensitive (in the limit) to wide variations in initial microstates.
> (Railton 1981: 251).

In classical statistical mechanics, the underlying thermodynamic systems are deter-
ministic. Thus in any particular situation the system in question has some particular
set of initial conditions or other, not a probability distribution over initial conditions.
Together with the laws of mechanics, these initial conditions determine the future be-
havior of the system. Presumably, this is the story the ideal explanatory text will tell;
the probability distributions of statistical mechanics will find no place here.

This is not the place to tackle foundational issues in statistical mechanics. I intro-
duce the example only because it illustrates the provision of explanatory information
without supplying portions of the ideal text, and it suggests how Railton thinks this
can proceed. I think the suggestion has merit. The next two sections will be devoted
to exploring some specific examples, with an eye toward the ways in which these the-
ories put constraints on the causal possibilities and the various roles this explanatory
information can play.

5. Circumventing the Ideal Explanatory Text

The general strategy behind explanations that obviate the need to reproduce the ac-
tual ideal text is the following. A system's being in a certain state is explained by
showing that, given the satisfaction of certain constraining assumptions, the system will
be in that state regardless of the particular causal details at work. An instance of such
an explanatory strategy is what Sober (1983) calls "equilibrium explanation". As he
puts it, "Where causal explanation shows how the event to be explained was in fact pro-
duced, equilibrium explanation shows how the event would have occurred regardless of
which of a variety of causal scenarios actually transpired." (Sober 1983, p.202).

A classic example of equilibrium explanation is Fisher's treatment of sex ratios.
Fisher explained the prevalence of a 1:1 sex ratio in nature by illuminating a modal fea-
ture, to use Railton's terminology, of the causal processes that determine sex ratios. He
used an optimality argument (in this case with fitness a function of reproductive success
at the level of grandoffspring) to show that the 1:1 sex ratio is a stable equilibrium with
regard to natural selection. When populations deviate from this ratio, offspring of the
minority sex will give the parent higher expected reproductive success at the level of
grandoffspring (i.e. the fitness of the parent is enhanced more by producing an offspring
of the minority sex than of the opposite sex). Thus deviations from the 1:1 ratio set up
differential selection pressures (selection for producing the under-represented sex and
against producing the common one), and these pressures will (if natural selection is not
interfered with by other evolutionary forces) bring the system back to the 1:1 ratio.
(See Fisher 1931 for the detailed development of this argument.)

The guiding idea behind Fisher's argument is that (1) male and female offspring con-
tribute to the fitness of the parent in different ways and to different degrees as the cir-
cumstances vary, (2) as a consequence, the fitness gain per unit of resource (in whatever
currency one chooses to measure resources) allocated to the production of males versus
females can itself vary with the circumstances, (3) selection will always favor (again *ce-
teris paribus*) the optimal use of resources, (4) therefore, the equilibrium situation will

be, as Stearns (1982, p.626) puts it, "...equal allocation to fitness gained through male and female routes." The 1:1 sex ratio is but one application of this idea, and a more systematic treatment has resulted in a general theory of sex allocation (Charnov 1982).

Equilibrium approaches such as Fisher's sex ratio argument and its generalization to sex allocation theory are themselves special cases of an explanatory strategy which involves the invocation of fitness differences to account for certain characteristics of a population. As such, equilibrium approaches are not without their foundational controversies, but setting these issues aside, it seems clear that to the extent they are successful, they succeed by eliminating the need to know the actual causal story. In Sober's words, "...Fisher's account shows why the *actual* initial conditions and the *actual* selective forces don't matter; whatever the actual initial sex ratio *had been,* the selective pressures that *would have* resulted would have moved the population to its equilibrium state" (Sober 1983, p.202).

Fisher's treatment of sex ratios has contributed to our understanding of biological phenomena in a number of ways. It provides a kind of theoretical derivation of an initially surprising empirical regularity - the prevalence of 1:1 sex ratios in natural populations. It has served as a kind of paradigm for "fitness explanations" in a wide range of areas, and it has given birth (to pursue the reproductive theme) to a large family of theoretical models - sex allocation theory. And it has achieved these significant advances in understanding without making actual reference to the causal mechanisms and processes which underwrite the phenomena to which it is applied.

The theory of island biogeography furnishes another example of an equilibrium explanation. Developing ideas expressed in Preston (1962), Mac Arthur and Wilson (1967) constructed a simple mathematical model for representing the equilibrium number of species on an island. In its simplest form, the theory can be given the following verbal characterization. Ignoring speciation, immigration is the only way to add species to an island and extinction is the only way to take them off. (There are difficulties involving when to count species as established residents, but I will skip over these details.) Immigration and extinction rates themselves depend on a number of things. For example, immigration rates are negatively correlated with species number. One reason is essentially analytic; given a roughly fixed pool of candidate colonists, as the number of species on the island increases the probability that a new arrival is also a new kind decreases. Similar considerations imply that the extinction rate should be positively correlated with species number. If there is always some positive probability of extinction, then the probability that some species will go extinct increases as species number increases. If one assumes that these probabilities depend only on relative frequencies, then the situation can be represented graphically as follows with I as immigration rate and E as rate of extinction:

Number of Species
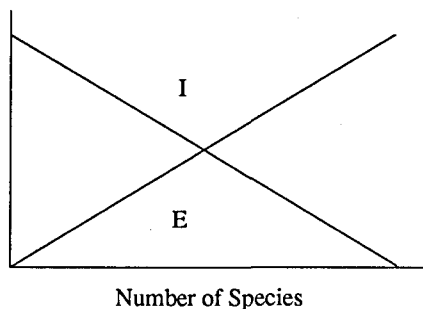
The linear relationships depicted in the above figure make the patently unrealistic assumption that all species have equal probabilities of colonization and extinction. MacArthur and Wilson point out that the immigration rate will fall more rapidly in the initial stages of colonization (with low S) as the island gets filled up with the good colonizing species. In addition, competition and the increased extinction probability associated with smaller population size should accelerate the extinction rate with higher values of S. These considerations change the shapes of the immigration and extinction curves (though they are still supposed to be monotonic). Other considerations suggest that different curves should be associated with different situations. For example, overall immigration probability should be lower as the distance from the immigrant pool increases (because immigration becomes more of a feat). Also, again owing to the effects of small population size on extinction rates, overall extinction probability should increase as the size of the island decreases. These additional ideas can be incorporated into the graph as follows:

Number of Species
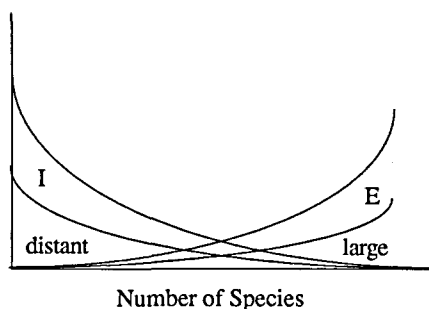
As is obvious from the graph, because immigration rate is a monotonically decreasing function and extinction rate is a monotonically increasing function, the point at which these two curves intersect is a globally stable equilibrium. In addition, the equilibrium species number ranges from lowest values in small, distant islands to highest values in large islands close to the source pool of immigrants.

This is only a brief sketch of the core of the theory of island biogeography, but it can also be used to illustrate the way in which equilibrium explanations can be applied to empirical regularities. One of the "phenomenological laws" of biogeography has it that, other things equal, the smaller the island, the fewer the number of species it will contain (roughly in the ratio of a tenfold reduction in area equalling a reduction in the equilibrium species number by one half). Another empirical rule is that, among islands of comparable size, the further from the immigrant pool, the lower the species number. The explanation of these regularities in terms of island biogeographic theory is the following. Whatever the actual mechanisms determining species diversity on islands, they will act by influencing immigration and extinction rates, and they will push the island toward the equilibrium value at which immigration balances extinction. Furthermore, as the graph illustrates, the different curves associated with different situations suggest different equilibrium values in these situations, with smaller size and greater isolation both working to lower the value. The empirical rules, then, reflect the fact that the balance between immigration and extinction has most islands around their equilibrium value, and these values form the pattern that they do because of the effects of area and degree of isolation on the immigration and extinction curves.

To focus on the theory of island biogeography as an explanation of the empirical rules concerning species diversity on islands is to ignore what is perhaps most signifi-

cant about this theory, namely, its importance as a catalyst for further theoretical development (Haila and Järvinen 1980). In fact, getting the empirical generalizations right (to the extent that it has them right - itself a matter of significant controversy) may be more significant for its validation of the model as a good way to think about phenomena such as species number, than for its ability to clarify what was initially puzzling.

The island biogeographic account of species number is a less perfect example of equilibrium explanation than Fisher's sex ratio argument. As we saw, Fisher's argument was quite independent of the causal details, provided that natural selection was the primary force at work and the population in question satisfied certain basic assumptions (which were not discussed). The account was independent of the mechanisms generating the selection forces. There is less independence of this kind in the biogeographic case. It is true that immigration and extinction rates are properties which supervene over a wealth of causal detail, but as these properties are represented in the simple version of the theory under discussion, they do not supervene over everything causally relevant to immigration and extinction. The theory tells us what the immigration and extinction curves will look like *provided that* area and distance from the colonization source are the major causal influences. But there are a variety of other factors which can affect the shapes of these curves, for example, factors that affect habitat heterogeneity such as variations in altitude. To discuss these complications, and the theoretical refinements they have spawned, would take us too far afield. The point is that, in the absence of any way to model these additional factors, the model is restricted (in causal terms) to certain kinds of causal situations. The equilibrium explanation of species number works by referring to some of the causal details; it tells us the actual causal story doesn't matter so long as that story talks about island sizes and distances from the source pool of immigrants.

Despite the fact that the island biogeographic example distances itself less from the ideal explanatory text than the sex ratio argument, it still makes use of what I have been calling radically supervenient properties. Immigration rate for example, as it is understood in the general theory, supervenes over a wide range of physical situations - the stories behind a given immigration rate are as varied as the dispersal mechanisms of organisms. But, as in the case of fitness, a recapitulation of the causal account behind the number of species on a given island is not likely to be augmented by attributing a certain species immigration rate to the island. The account may well make use of the rate at which particular species immigrated, but with the species specific rates in hand there is no information for the overall immigration rate to add. The theory sets a modal constraint on how the species specific rates are likely to behave, but the ideal text reveals how they actually behave.

6. More Roles for the Possibilities

Next I would like to take up two examples which involve the application of the basic Lotka-Volterra model of competition;[5] the examples also differ from the earlier ones in that they exemplify applying theoretical results to more specific situations. Competition theory speaks to the conditions under which a community of competing species can coexist in a stable equilibrium. In particular, one of these conditions states that there cannot be more species in the community than there are resources. The first example I will discuss involves an apparent anomaly with this theoretical result. As will be seen, it illustrates the way in which the theoretical construal of the possibilities can fruitfully direct investigation away from situations covered by the theory.

In a paper entitled "The Paradox of the Plankton", G. E. Hutchinson (1961) described a situation which appeared to violate the condition on resources. Hutchinson

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observed that there appeared to be many more species of phytoplankton coexisting in lakes and marine waters than there were resources that were limiting for these populations. There are a number of possible responses to this theoretical anomaly. One is to maintain the equilibrium by modifying the theory. Competition is only one of the forces alleged to be responsible for community structure. Perhaps trophic relationships, for example, must be included. This was not Hutchinson's response; he rejected the equilibrium assumption and attempted to explain the diversity of the phytoplankton in terms of the temporal variation in resources. In brief, his idea was that the lake actually represented a temporal succession of different environments in which different species were competitively superior, with the various species getting through the hard times by a variety of mechanisms (e.g. diapause).

What is important for our purpose is neither Hutchinson's particular response nor its success, but rather the way in which the theory provides a framework from which to approach the phenomena, a framework which suggests the kinds of observations which ought to be important. Given the paucity of distinct resources in the relatively unstructured pelagic environment, competition ought to be intense. But its consequences are not apparent. For someone committed to the classical theory, the obvious move is to look for some mechanism that is neutralizing the competition. In this case, Hutchinson's proposal was that before the consequences of competition could be manifested the environment changed, ushering in a new set of competitive dominance relations. Since Hutchinson's early paper, ecologists have devoted a great deal of effort toward a theoretical treatment of environmental heterogeneity in both space and time. The paradox of the plankton shows how a theory can have explanatory virtue even in cases where it breaks down (that is, the theory is important for what it says is impossible). The final example is intended to illustrate the way in which theory can have explanatory virtue by bringing some particular phenomena under its domain.

In a spirited defense of the theoretical approach to community ecology, Roughgarden (1984) draws on an example from his own research to illustrate the way in which theory (in this case classical competition theory) can provide a framework from which to address particular problems. The island of St. Maarten in the eastern Carribean is inhabited by two species of lizards in the genus *Anolis*. The larger of the pair, *A. gingivinus*, occurs throughout the island, while the smaller *A.wattsi* is restricted to higher elevation inland habitats. Roughgarden hypothesized that the absence of *A. wattsi* from the lower elevations is due to the competitive superiority of *A. gingivinus* in these locations. Casting this problem in the framework of classical competition theory is useful because "...The Lotka-Volterra competition equations help us to visualize how competitive exclusion occurs as a population process, and thereby aids in planning the research to determine if this hypothesis is true." (Roughgarden 1984, p.16).

But how does the theory play this role? The paradox of the plankton illustrates the way in which having theoretical expectations thwarted - in this case the theorem of classical competition theory which says the number of species cannot exceed the number of limiting resources - can ultimately advance understanding. But the utility of theoretical models is not confined to isolating particular situations to which the model does not apply. Perhaps the most significant use of theory is to model real situations, that is to describe some situation in such a way that it is, in fact, a model of the theory. In this case one must first be satisfied that the theory applies, and this means evaluating the assumptions of the theory for the situation at hand. These assumptions themselves provide a conceptual jumping off point; as I will attempt to illustrate, this is, I think, at least part of what Roughgarden has in mind.

The discussion of the assumptions of the theory and their satisfaction by the *Anoles* on St. Maarten will be selective and greatly oversimplified, a much more thor-

ough account is in Roughgarden (1986). At the heart of classical competition theory is the idea that the magnitude of competition between two species is proportional to the degree of overlap in their use of resources. If the patterns of resource consumption exceed a certain degree of limiting similarity then the theoretical expectation (excluding the possibility of evolutionary adjustments in these patterns) is that the two species will not be able to coexist. This is the competitive exclusion of Roughgarden's hypothesis. Thus, applying the theory means determining which resources are limiting and uncovering the patterns of utilization of these resources. A variety of studies of Carribean *Anoles* have revealed that food is a limiting resource, that it is partitioned in terms of prey size (with a correlation between body size and size of prey taken), and that among competing species the competition is asymmetrical, with the edge going to the larger species. These findings come down in favor of the interpretation of the distributional patterns on St. Maarten as an example of competitive exclusion. There is a great deal more to the story however; the theory also assumes that competition among *Anoles* is the major ecological factor at work, that the populations are essentially closed to immigration, as well as more technical assumptions such as that the competition coefficients in the competition equations are in fact constants and not themselves functionally related to population densities and the like. Satisfying oneself that these assumptions are reasonable sets up an entire agenda of empirical studies. As already noted, a thorough discussion of the *Anole* community on St. Maarten, and the extent to which they satisfy the assumptions of the theory, is in Roughgarden (1986). What I am emphasizing here is the way in which the theory supplies the conceptual categories that structure the investigation, for example, by focusing efforts on patterns of resource utilization.[6]

As with optimality models and the models of biogeographic theory, classical competition theory makes use of radical supervenience. To say, for example, that the competition coefficient relating two species has a certain value is to refer only indirectly to actual causal processes; the processes are those (whatever they may be) in terms of which the population density of one species is causally relevant to the population density of the other. The causal relevancies may be realized through a wide variety of mechanisms, but it is the mechanisms that would occupy the ideal text. Theoretical concepts such as competition coefficients, intrinsic rates of increase, and carrying capacities do not add anything once the causal details are in place.

7. Conclusion

Theories can supply explanatory information without providing details about causal mechanisms and the underlying causal regularities governing these mechanisms. Bringing a class of phenomena under a theoretical model can increase our understanding of that phenomena, and it can do so even if the theoretical model has no chance of being a causal model (because it fails to make reference to the actual causal details). As we have seen, this understanding can take a variety of forms. Equilibrium explanations do an end run around the ideal text - with differing degrees of thoroughness. In the process, what does supervenient theory deliver: derivations of "phenomenological laws", theoretical extensions, exemplification of model building strategies in new domains, theoretical expectations which can serve as a guide to empirical anomaly, and an organized conceptual framework (complete with the capacity for mathematical treatment) to bring to bear on particular situations.

We have put more flesh on the "role of theory" question with which we began. The philosophical challenge is to understand how theory can play this role. In some ways the models we have been discussing have an heuristic function,[7] but heuristics alone (whether it is an objective affair or not) seems an insufficient ground for

achievements such as Fisher's treatment of the sex ratio. The challenge, as I see it, is to account for the objectivity of theoretical explanation, while accommodating the fact that the theories involved organize causes simply by their effects. If no details about causal antecedents are forthcoming - because there is nothing systematic to be said about them - then it does not seem possible to regard such theories as approximating causal regularities. This poses a problem for causal theories of explanation such as Salmon's. How else might we ground the explanatory virtue? The second of Salmon's "two venerable intuitions" about scientific explanation, the covering law approach, needs a re-tooling of an already overworked device - the law of nature - in order to succeed. A third possibility is to adopt the deductive systematization idea without the associated covering laws. This is essentially the strategy pursued by Kitcher. Since the laws were the source of objectivity on the covering law view, something must take their place. For Kitcher it is the systematization that the methodology of unification takes us to in the limit. Whether Kitcher's account fares any better in the grounding of theoretical explanation is a question for another occasion. This much can be said however - the success of any account of theoretical explanation turns, in part, on how adequately it enables us to understand the efficacy of the various roles for theory discussed above.[8]

Notes

[1]The parties involved include Mills, Beatty, Brandon, Rosenberg, Williams and Sober. See Cooper (1988) for details.

[2]Sober, for example, denies that these radically supervenient properties are physical properties, yet he seems to think that they capture the laws that Laplace's demon would miss. This is part of the controversy referred to in footnote 1.

[3]At least not "fundamental and comprehensive" enough for us, as epistemic agents.

[4]I offer a challenge to those who would challenge causation, as well as a more detailed discussion of ideal explanatory texts in Cooper 1989.

[5]Considerations of space preclude a description of this model.

[6]See Haila (1986) for an elaboration of similar ideas.

[7]Wimsatt (1980), for example, puts a good deal of stress on the heuristic value of theoretical models.

[8]I discuss this issue in Cooper (1989), in the context of arguing for a two virtue theory of explanation (with theoretical explanation and causal explanation as two distinct vehicles for the advancement of understanding).

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