

Ecological Stability, Model Building, and Environmental Policy: A Reply to Some of the Pessimism¹

Recently, there has been a rise in pessimism concerning what theoretical ecology can offer conservation biologists in the formation of reasonable environmental policies. In this paper, I look at one of the pessimistic arguments offered by Kristin Shrader-Frechette and E. D. McCoy (1993, 1994)--the argument from conceptual imprecision. I suggest that their argument rests on an inadequate account of the concepts of ecological stability and that there has been conceptual progress with respect to complexity-stability hypotheses. Such progress, I maintain, can supply important resources for conservation biologists in determining environmental policies.

I. Introduction. There has been a recent pessimism (Peters 1991, Shrader-Frechette and McCoy 1993, Sagoff 1992, Sarkar 1995) arising among some biologists and philosophers as to what theoretical ecology can offer environmental policy. As one such example, Kristin Shrader-Frechette and E. D. McCoy (1993, 1994, 1995) argue that community ecology is incapable of providing theoretical resources for preserving species, communities, and ecosystems. There are several arguments that Shrader-Frechette and McCoy offer and I will focus on one--the argument from conceptual imprecision. I respond to this argument by showing that it depends on an incorrect account of ecological stability concepts and that there has been important conceptual progress in modeling complexity-stability relationships. Furthermore, I sketch how theoretical ecology can in virtue of this progress supply important resources for formulating reasonable environmental policies.

II. Conceptual Imprecision and Complexity-Stability Hypotheses. Community ecologists have debated what are the appropriate meanings of terms like *community* and *stability* for some time. Ecologists have thought that communities are superorganisms, functionally interrelated feedback systems, and statistical assemblages bounded by space

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and time. Stability has been thought of as the return of species abundances to their equilibrium values from perturbations, resistance of invasion by exotics, and the persistence of species composition of the community after a disturbance. At first glance, one might conclude that all is in conceptual disarray in community ecology since ecologists cannot even agree on what they are theorizing about.

Kristin Shrader-Frechette and Ed McCoy argue (1992, 1993) that the terms *stability* and *community* are “ambiguous, imprecise, and inconsistent.” They claim that if community ecology is to produce predictive, general theories that are adequate for environmental applications, then the foundational concepts of ecology must be clear and precise. If these foundational concepts are unclear and imprecise, then there will be conceptual confusion, and different interpretations of those concepts will lead to different conservation strategies (1993, 54, 57-8). They conclude that the theories of community ecology are not well equipped for conservation purposes. In this essay, I focus on ecological stability concepts and not community concepts; however, my arguments concerning the former are very similar to those I would give with respect to the latter.

Ecologists have become more and more concerned with providing a precise notion of ecological stability over the last few decades, especially given the continual interest in the “balance of nature,” and the “diversity/complexity-stability hypothesis”—the hypothesis that as the diversity or complexity of a community increases so does the stability of the community. Every few years a new review article appears which articulates the latest notions of ecological stability. For example, Gordon Orians (1975, 141-2) lists seven different “stability concepts”: constancy, persistence, inertia, elasticity, amplitude, cyclic stability, and trajectory stability. In order to substantiate Shrader-

Frechette and McCoy's claims, it is useful to look at the work of community ecologist Stuart Pimm. Pimm (1984, 1991) has articulated the most complete framework of stability concepts to date.

Pimm distinguishes between definitions of *complexity*, *stability*, and the *variables of interest*. The complexity of a community can be defined in terms of species richness, connectance, interaction strength, or evenness. Species richness is the number of species in a community. Connectance is the number of interspecific interactions divided by those possible. Interaction strength is the mean magnitude of interspecific interaction; i.e., the size of the effect of one species' density on the growth rate of another species. Species evenness is the variance of the species abundance distribution. The variables of interest are individual species abundances, species taxonomic composition, and trophic level abundance.

The "stability" of a community is thus characterized in one of the following ways (see 1984, 322).

- A) Stable: a system is stable just in case all the variables return to their initial equilibrium values following a perturbation.
- B) Resilience: how fast the variables return to their equilibrium following a perturbation.
- C) Persistence: how long the value of a variable lasts before it is changes to a new value.
- D) Resistance: the degree to which a variable is changed following a perturbation.
- E) Variability: the degree to which a variable varies over time.

We can think of the number of options for formulating a complexity-stability hypothesis as having the three dimensions of complexity, stability, and variable of interest. There are four definitions of complexity, five of stability, and three variables of interest. This leads to a very large number of combinations of concepts. Thus, there is an

extremely large number of contenders which might undergird the complexity-stability hypothesis. As a result, the most recent conceptual work of a community ecologist seems to confirm Shrader-Frechette and McCoy's claim that there are many different meanings of the stability concept.

The five meanings as outlined by Pimm (1984), do not even describe all alleged characteristics of communities; some of the meanings refer to the time during which community changes take place, rather than to the changes itself, and some of the concepts presuppose different spatial and temporal scales than others... There is no homogeneous class of processes or relationships that exhibit stability or that define a community, and there is no single, adequate account of what either community or stability is (1993, 57-8).

Not only are there are a large number of contenders for *complexity*, *stability*, and variables of interest but different combinations can lead to very different conservation strategies (1993, 52-5). Imagine that we have a community that is composed of a set of species and each species is a metapopulation (populations of each species are separated geographically with some migration). One strategy is to maintain the equilibrium densities of each population of a species in a community. In this case, stability of a species is the return of each population to its stable equilibrium, complexity is species richness, and the variable of interest is species abundance. Another strategy is to maintain the average species richness where stability is variability, complexity is species richness, and the variable of interest is species abundance. Thus, in the former case, we would try to minimize the fluctuations in densities of each population. In the latter case, we would allow for fluctuations in different populations of the species but maintain the average species density. Hence, different concepts of community, complexity, and stability can lead to different conservation strategies.

To the degree that ecological concepts (and theories) differ, to the same extent do

the strategies and conclusions of applied ecology differ. If our ecological concepts (and theories) are uncertain, then so are our applications (Shrader-Frechette and McCoy 1993, 54)

It seems that *stability* has many different meanings and hence ecological theories are imprecise and inapplicable to environmental policy. Moreover, if *stability* has many different meanings, then theories that employ stability concepts will lead to different conservation strategies. It appears then that theoretical ecology, more specifically complexity-stability hypotheses, cannot provide aid to conservation biologists.

There is an alternative to the claim that all is in conceptual disarray in community ecology. Shrader-Frechette and McCoy confuse different *types* of stability, and hence different *stability* concepts with a single *stability* concept with multiple meanings. Shrader-Frechette and McCoy do not specify what conceptual imprecision is but it seems that the following is true: conceptual imprecision occurs if (1) distinct concepts are treated as being the same or vice versa, (2) the same term is inappropriately used to apply to several different concepts, and (3) different terms are inappropriately used to apply to the same concept. In order to see that their alternative is untenable we do not need a sophisticated theory of concepts here but only truisms. Two purportedly different concepts are the same concept only if they have the same instances. Likewise, a concept *entails* another just in case every instance of the former is an instance of the latter. Hence, two concepts are distinct if they are not “coextensive.”

A community is *equilibrium stable* (what Pimm calls “stability”) if and only if all of the species abundances return to their stable equilibrium after a perturbation. A community’s resilience stability is determined by how fast the variable of interest returns to its pre-perturbed stable equilibrium. So, a community *x* is more *resilience stable* than a community *y* just in case both are equilibrium stable and *x*’s variable of interest returns

faster to its stable equilibrium after being perturbed than y 's. If a community is more resilience stable than another is, then both are instances of the concept *equilibrium stability*. Hence, two communities which are instances of the relational concept *resilience stability* entails that separately they are instances of the *equilibrium stability* concept even though converse does not hold. More exactly, if two communities are equilibrium stable it does not follow that one is more resilience stable than the other. Thus, the concept *equilibrium stability* is distinct from the relational *resilience stability* concept.

As another example, the persistence stability of a community is determined by how long the variable of interest maintains a particular value. So, a community x is more *persistence stable* than a community y just in case the value of the variable of interest of x lasts longer than that of y . The relational *persistence stability* concept is distinct from the *equilibrium stability* concept. Two communities may instantiate the former and yet neither might be equilibrium stable. Different stability concepts bear interesting relations between one another; however, they are distinct. Since every equilibrium stable communities x and y can instantiate the concepts of resilience stability, persistence stability, resistance stability, and variability stability at the same time, then the concepts are distinct and non-competing. A community can possess these different sorts of stability in a piecemeal fashion. In the same way that philosophers of biology have argued that there are different *gene* concepts such as Mendelian genes, molecular genes, and evolutionary genes we can see that a similar phenomenon exists with respect to stability concepts. Pimm, Orian, and other ecologists treat distinct concepts as distinct so it is reasonable to think that the first sort of conceptual imprecision is not present.

Shrader-Frechette and McCoy could agree there are several *stability* concepts

which are distinct and individually precise. However, they still might contend that that there is conceptual imprecision because different terms are often used for the same concept. As we have seen, Gordon Orians' account (1975, 141-2) has seven stability concepts and only one that uses the same word as Pimm's--*persistence*. A response to this worry is that even in those circumstances where ecologists use different terms for the same concepts, they often implicitly agree with one another. For example, Orians and Pimm both have terms for a variable's return to equilibrium (trajectory stability, stable), the speed with it returns to equilibrium (elasticity, resilience), the time during which a variable maintains the same value (inertia, resistance), the area over which a system returns to equilibrium (amplitude, local and global stability) and so on. Even though there are different terms used, the meanings of the terms are transparent since they each *explicitly* define their terms. Thus, conceptual imprecision is absent in this case because different terms are not used for the same concept *inappropriately*.

The final type of conceptual imprecision I mentioned was using the same term to refer to different concepts. Ecologists like Pimm and Orians have clearly not fallen prey to this sort of conceptual imprecision since they have provided different terms for the different concepts as we have seen. We can thus conclude that ecologists have treated distinct stability concepts as distinct, have not used different terms for the same concept inappropriately, and have not used the same term for distinct concepts inappropriately. Consequently, the sort of conceptual imprecision that Shrader-Frechette and McCoy allege does not occur in community ecology. There may be other types of conceptual imprecision but that remains to be seen.

I have argued that there is an alternative interpretation of ecological stability

concepts which is superior to Shrader-Frechette and McCoy's interpretation. If this alternative is correct, then it is false to claim that ecological stability concepts themselves are unclear and imprecise and it does not follow that ecological theories are of little use in the development of environmental policy. If there are different stability concepts, which lead models to predict different results, then we should also expect this to lead to different consequences in environmental policy as well. The fact that alternative conservation strategies arise if the concept of ecological stability is unclear and imprecise does not lend unequivocal support for their account. Alternative conservation strategies will also arise if there are clear and precise ecological stability concepts. Hence, we cannot conclude from the fact that there are alternative conservation strategies alone that their alternative is justified.

In the third section, I show that there is not the serious conceptual imprecision that Shrader-Frechette and McCoy allege. I suggest theoretical ecologists themselves successfully clarify different types of stability. Recent work on modeling complexity-stability relationships shows that community ecologists can nicely remove conceptual imprecision when it occurs. Nevertheless, there is still room for pessimism. Even if ecologists have clear, precise stability concepts it could still be the case that theoretical community ecology might still have very little to offer conservation biology and environmental policy. In the fourth section, however, I show that is not the case: recent work on modeling complexity-stability relationships can contribute to environmental policy.

III. Food Webs and Model Building. Robert May (1972) was one of the first to explore in a very precise way the connections between complexity and stability with local

stability analyses.² May assumes that we have a community with n species with densities $N_i(t)$ and the dynamics of the community may be described by a set of nonlinear first-order differential equations. In order to determine the possible equilibrium N_i^* of the species we set their growth rates equal to zero ($dN_i(t)/dt = 0$) and solve the equations. To study the stability of the equilibrium community we write,

$$N_i(t) = N_i^*(t) + x_i(t) \quad (1)$$

where $x_i(t)$ refers to the arbitrarily small perturbations to the equilibrium $N_i^*(t)$. If we give a Taylor expansion of the n equations around the equilibrium, we have a set of n linear first-order differential equations,

$$dx_i(t)/dt = \sum_{j=1}^n a_{ij} x_j(t) \quad (2)$$

where a_{ij} is the coefficient of interaction between species i and j which is the effect of species j on species i . Thus, if i is a predator and j is prey, then $a_{ij} > 0$ and $a_{ji} < 0$. If i and j are competitors, then $a_{ij} < 0$ and $a_{ji} < 0$. If i and j are mutualists, then $a_{ij} > 0$ and $a_{ji} > 0$. It is also possible that for some species i and j , $a_{ij} = 0$. We can describe the possible interactions among species i and j by the signs of a_{ij} . We can also represent (2) as

$$d\mathbf{x} / dt = \mathbf{A}x(t) \quad (3)$$

where \mathbf{x} is the $n \times 1$ column vector of x_i and \mathbf{A} is the $n \times n$ “community matrix” whose elements a_{ij} describe the effect of species j on species i near equilibrium. An equilibrium point is locally stable just in case all of the eigenvalues of the community matrix have

² However, in a more general context, see Gardner and Ashby (1970).

negative real parts.

May constructed his model communities with S species by choosing the interaction coefficients a_{ij} at random. Thus, some species interaction coefficients were greater than, less than, and equal to zero. He defined the connectance C of the community as the proportion of interspecific interactions a_{ij} not equal to zero. The intensity I of the interspecific interaction a_{ij} was a random variable with a mean of zero and a variance of I^2 .

May demonstrated that a community is qualitatively stable if, and only if,

$$I(SC)^{1/2} < 1 \tag{4}$$

Hence, an increase in the number of species, connectance, and interaction strength all lead to a decrease in the stability of a community.

May's result has not gone uncriticized. For example, randomly constructed food webs contain predators with no prey and prey with no predators, which is biologically unrealistic. Likewise, randomly constructed food webs contain loops where species i feeds on species j , j feeds on species k , and k feeds on i which is also biologically unrealistic (Lawlor 1978).³ Even though the sharp transition from stability to instability as described by (4) does not obtain for more realistic models, these models lead to the same general result that stability decreases with increasing complexity. May's result seems to be robust.⁴

Pimm (1979) investigated larger perturbations than the arbitrarily small ones of May's analysis. Pimm's larger perturbation was the deletion of single species from the

³ For a discussion of the idealizations in May's models, see Pimm (1984, 67-73)

⁴ For similar results with different models, see DeAngelis (1975), Gipin (1975), and Pimm (1979).

community. A community is *species deletion stable* if, and only if, following the removal of a species from the community all of the remaining species are maintained at a new locally stable equilibrium (1982, 47). Interestingly, Pimm found that if only a basal species is deleted, the community's species deletion stability does not decrease with increasing interacting pairs of predators and prey. However, he found that generally the number of interactions decreases the community's species deletion stability (1979, 355).

In order to argue that Shrader-Frechette and McCoy's interpretation of ecological stability is incorrect, that there is not the conceptual imprecision they argue for, I present a particular example. This example demonstrates that community ecologists have not only recognized that there are different stability concepts but, with these concepts, recognize and prevent conceptual imprecision as well.

J. S. McNaughton (1977) examined how the popularity of the diversity-stability hypothesis had declined rather abruptly from the late sixties through the mid-seventies. He explained that this was largely the result of the mathematical modeling of May and others. However, he argued that to determine the truth of the diversity-stability hypothesis we must turn to empirical tests, anything else are "acts of faith, not science" (1977, 516). McNaughton examined several different experimental studies he and his colleagues had performed. One such study was conducted on grasslands in the Serengeti-Mara ecosystem in Tanzania and Kenya. McNaughton examined the effect of the grazing African Buffalo *Syncerus caffer* on the grasslands. There were several adjacent stands of plants, some of which were placed in fencing and hence were control stands, and some of which were unfenced and grazed by the resident Buffalo species. In the control stands, there was a more and less diverse community and the same was true of the grazed

stands.⁵

McNaughton found that that the resulting diversity of the more diverse, grazed community was significantly different than the more diverse, control stand, whereas the resulting diversity of the less diverse, grazed community was not significantly different than the less diverse, control stand. Species diversity in the more diverse stand decreased more than in the less diverse stand because of the grazing. Amazingly though, the more diverse community suffered less of a reduction in primary production (biomass) than the less diverse community. McNaughton hypothesized that if a community has many species that overlap in resource use and the community suffers a perturbation, then the “adjacent” species can compensate by utilizing the vacant resources. In the more diverse, grazed stand, *Themeda triandra* is a understory species in the tall grassland. As the grassland “canopy” was opened *T. triandra* was able to compensate for the consumption of the tall species and maintain the biomass of the community. McNaughton concluded from his study that, “[t]he weight of evidence resulting from explicit tests of the diversity-stability hypothesis...suggests, not that the hypothesis is invalid, but that it is correct” (1977, 522). He also explained that popularity of the diversity-instability hypothesis as resulting from the “less reliable” mathematical modeling and the too few empirical tests. It thus seemed to be true that species diversity stabilizes ecosystem properties like primary production and so the diversity-stability hypothesis is true and the recent mathematical modeling must be incorrect.

In 1983, Pimm and Anthony King replied to McNaughton’s work attempting to “resolve this apparent contradiction between theory and empiricism.” Pimm and King

⁵ Diversity in McNaughton’s study is not species richness but is estimated by the Shannon-Weaver diversity index, $H' = -\sum p_i \ln p_i$ where p_i is the proportion of individuals found in the i th species.

devised grazing food web models with n plant species and one herbivore. They utilized generalized Lotka-Volterra equations,

$$dx_i / dt = x_i \left(b_i + \sum_{j=1}^n a_{ij} x_j \right) \quad (5)$$

where x_i is the biomass of the i th species; b_i is the rate of change of biomass of species x_i in the absence of predators and prey; and a_{ij} is the effect of species j 's biomass on the growth rate of species i 's biomass. Pimm and King set the parameters b_i and a_{ij} with as much biological realism as possible (1983, 230-1) and examined the models with respect to three types of complexity--species richness, connectance (the number of competitive interactions between plant species out of those possible), and species diversity.

In order to examine these models, Pimm and King first determined those model communities whose species have a locally stable equilibrium with a positive biomass when the herbivore is present. They then removed the herbivore and determined which of those remaining model communities once again have a new locally stable equilibrium with a positive biomass. Pimm and King found that for each type of complexity, complexity increases relative biomass stability which is the ratio of total plant biomass without the herbivore and the total plant biomass with the herbivore. They also found that if stability is constituted by species composition of the community, then stability *decreases* with increasing complexity. So Pimm and King's and McNaughton's results generally coincide. Pimm and King draw the following conclusions from their study,

There is no paradox here: Our study addresses a different question than previous studies.... It may be surprising--but it is certainly not impossible--that more connected systems are both more likely to change in composition yet less likely to change in total biomass following the removal of a species from the system.... The idea of systems possessing different kinds of stability and each changing

differently with complexity has also been made by Armstrong (1982) using a very different modeling approach (1983, 238).

Pimm and King argued that McNaughton was incorrect in supposing that either the field ecologists or the modelers were right. Once we recognize that there are different types of stability and that increasing complexity can increase/decrease those different types of stability independently, then we can diagnose the apparent conflict between the work of McNaughton and the modelers. Pimm and King do exactly what my alternative account of ecological stability concepts would recommend. They recognize that there are different types of stability and they use these different stability concepts to repair the conceptual confusion in McNaughton's arguments. This is significant because it shows that ecologists distinguish between different types of stability. Moreover, this has led to the removal of conceptual imprecision contrary to Shrader-Frechette and McCoy's arguments.

In this section, I have argued that the work of community ecologists, the modeling of complexity-stability relationships and food webs, has been conceptually precise. Ecologists recognize that there are different notions of stability and that can lead to different results. This conceptual precision has allowed ecologists to rid themselves of conceptual confusion. In the next section, I will argue that recent theoretical work in community ecology is important for formulating appropriate strategies for the preservation of species, communities and ecosystems, contrary to Shrader-Frechette and McCoy's assertions.

IV. Models, Conservation Biology, and Environmental Policy. Shrader-Frechette and McCoy argue that theoretical ecology does not provide important resources for developing environmental policy. I have shown that their argument from conceptual

imprecision is unsound and hence one of their reasons for pessimism concerning the work of theoretical ecologists is laid to rest. Moreover, I have tried to show that the work on the complexity-stability hypothesis has been conceptually progressive. Now I turn to how this progress is relevant to environmental policy. Shrader-Frechette and McCoy argue that the diversity-stability hypothesis has not contributed to environmental policy.

One of the best illustrations of how, despite its heuristic power, general ecological theory has failed to provide a precise, predictive basis for sound environmental policy is that of the diversity-stability hypothesis (1993, 3).

The complexity-stability hypothesis has not led to a precise predictive basis for environmental policy. This should not surprise us since for a variety of complexity and stability concepts, the hypothesis is probably false. However, it does not follow from the fact that the complexity-stability hypothesis is false for most stability concepts that *theoretical work* on complexity-stability hypotheses cannot contribute to the development of environmental policy. We have seen that for many models the stability of a community decreases with increasing complexity. This is a remarkable result since as Shrader-Frechette and McCoy recognize,

...the diversity-stability theory has been, by far, the most basic and the most persuasive of the utilitarian arguments for environmental protection.... Policymakers and scientists repeatedly have trotted it out as a rationale for environmental policies designed to save species in a given area. Numerous decisionmakers, for example, have cited the diversity-species thesis as grounds for supporting the Endangered Species Act (1993, 4).

Models may not provide definitive answers to particular conservation problems but they can help determine when an environmental policy is *not* based on a scientific rationale. The complexity-stability hypothesis has been shown to be far more complex than originally assumed--namely, that there are different types of stability and that for several

of these notions, stability actually decreases with complexity. Thus, any conservation policy that presupposes the complexity-stability hypothesis is true would be careless. It behooves conservation biologists and environmental decision-makers to concern themselves with theoretical ecology if they want to better understand the relations between complex communities and their stability. Theoretical community ecology can provide a much needed resource even when it does not give definitive answers about what to do in particular cases but only explores possibilities (Brandon 1991).

Theoretical ecology can also provide important guidelines for advice on particular conservation strategies. As an example, one of the most important problems of the current environmental crisis is that of the introduction of exotic species. The control and removal of these species from communities is expensive and may often be impossible. So, it is important to determine what species are more likely to invade certain communities and what effects they will have on endemics.

The work we have looked at on community food webs is important in answering these questions because those models are formulated to deal with questions about the effects of species additions and removals--i.e., perturbations and species deletion stability. On the basis of this theoretical work, Pimm and Gilpin (1991) argue that there are three "don'ts" suggested by the models. Impacts of exotic species will be severe if (1) the species is introduced into a community for which it has no predators, (2) the species is introduced in a community and is a polyphagous species, and (3) the species is introduced into a community which is relatively simple where the removal of a few plant species will cause the entire food web to collapse (1991, 301-2). These are important recommendations, which do provide guidance about how to deal with particular species

in particular communities contrary to what Shrader-Frechette and McCoy say. As Pimm and Gilpin write,

We do not pretend that our models will prove to be perfect; our science is too young, our study systems too multivariate. Nonetheless, our models are greatly superior to ignorance. And, in employing our models and theories against the challenges of the environmental crisis, we will have the best possible chance to test and to correct our theoretical understanding (1991, 303).

IV. Conclusion. In this essay, I have suggested that Shrader-Frechette and McCoy's argument from conceptual imprecision is unsound. There are a variety of stability concepts and ecologists have begun to systematically explore and use them to remove various confusions concerning the complexity-stability hypotheses. I have argued that theoretical community ecology is important for environmental policy. A variety of precise stability concepts exist that allow theoretical ecologists to probe complexity-stability hypotheses and provide important considerations for policy.

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