Critical Transtions in Ecology

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Abstract

In complex systems the degree of homogeneity (vs. heterogeneity) and connectivity (vs. modularity) determines whether or not there is a phase transition from one state to another. These are called critical transitions, and there are current efforts to understand both what factors are significant in causing these transitions and what factors are significant in predicting the fragility of these systems, or the susceptibility to the induction of a phase transition by some external shock. Complex phenomena in a wide range of fields can be studied using these ideas combined with the idea of critical slowing down. Approaches to complex systems in several examples will be discussed, with a focus on living systems.

1 Introduction

The Oil Embargo in the 1970s caused a period of what economists called "stagflation", where currency was inflating and the economy was stagnant. One of the first principles of macroeconomics I learned in high school was that inflation was not detrimental to the economy as long as it was anticipated; that is, only unanticipated inflation would cause unplanned loss of value to businesses and individuals. Prediction, it seems, is then the necessary condition on which stability lies.

Predicting the behavior of such complex systems as the global economy is what makes Warren Buffett a genius, and the inability of the general population to do so is what makes Buffett a billionaire. The ability to predict the trends of, for lack of a better word, "unpredictable" systems, especially large changes thereof, is a growing area of research stemming not from stock brokers but from physicists studying the universal behavior of physical systems undergoing phase transitions. Using scaling laws and critical behavior, physicists are able to derive not long term averages but particular behavior near phase transitions in what is called the critical region. The universality of these behaviors across a wide variety of systems, including our focus here of ecology, makes this interface of physics theory go beyond scientific experiment to everyday experience on an individual and global scale.

Ecology is in many ways like the economy [1]. Both must allocate scarce resources. Both experience outside forces; the economy: political and social; ecology: climatological and anthropological. Both feed back into those outside forces in a complex interplay. Both have many layers of complexity; from buying a newspaper to multinational trade unions, from microbes to jungles to climate change. And both experience critical transitions: stock market crashes, and population collapse. I refer back to the analogy of the economy not as a distraction, but as a constant reminder of the significance of the expanded scale of the study of critical transitions.

I should note here before we begin that even in ecology, there has been significant work on many systems. To get an idea of the work being done in this field, instead I propose to highlight just a few of these areas, and comment on the general insights that can be understood from that work and similar efforts on critical transitions in ecology. First, though, we should understand the connection of these studies and behaviors to physics.

2 Theory

In physics, critical regimes are characterized by the divergence of the correlation length to infinity, by critical slowing down, which is the increase of the relaxation time of the system due to small perturbations, crossover regions, and the presence of an order parameter.

We jump quickly[1] to the 1970s, where catastrophe theory is developed and

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[1] I apologize for the quick jump away from physics, but hopefully the relevant concepts to critical phenomena will become clear in the following examples.

criticized. Papers by Zeeman [2] and others develop the concepts of different types of catastrophes: folds, cusps, butterflies, and others, that exist in some parameter space of the system versus time. These bifurcations represent a picture of critical transitions when combined with flickering, or the tendency of a state to flip from one state to another.

In ecology, critical transitions are characterized by one-way, catastrophic failure of some stable state to another stable state. In our economy analogy, this is something like a stock market collapse or a bank run. Here, a positive feedback loop causes a system with comparatively long recovery time to drop increasingly rapidly in population or health. Notably, for systems near the critical regime, it does not take a significant outside forcing to cause a significant change in state. This susceptibility is what those who seek to prevent such collapses hope to measure by some indicator which changes behavior in the critical regime. Scheffer, et al. [3] summarize the parameters nicely, in figure 1. We can see a parallel between the ideas of modularity vs. connectivity to the idea of long range order. In systems where there is no long range order (hence modular, or disconnected regions dominate), there is no complete collapse, just independent collapses of smaller connected elements. This results in, as Scheffer notes, adaptation and gradual change. Here there is no increased susceptibility, and hence no critical regime to examine. On the other hand, connected systems have long range order, meaning that a perturbation in one space or time locality will propagate through a non-vanishing part of the system, and cause, if the susceptibility is high, a critical transition. If the susceptibility is low, however, the system is stable globally, and local perturbations are "repaired". This susceptibility is indicated by critical slowing down, or the inability of a system to "repair" itself over time. [4]. Homogeneity or heterogeneity within an ecological system can be compared to something like a single crystal or multiple domains. Having domain walls or heterogeneity decreases the likelihood of propagation of some perturbation across the system, and hence are important in determining the susceptibility of the system.

Scheffer also nicely summarizes the wide applicability of the study of critical transitions to many fields including finance, as we have mentioned, and other fields in a table. [3]

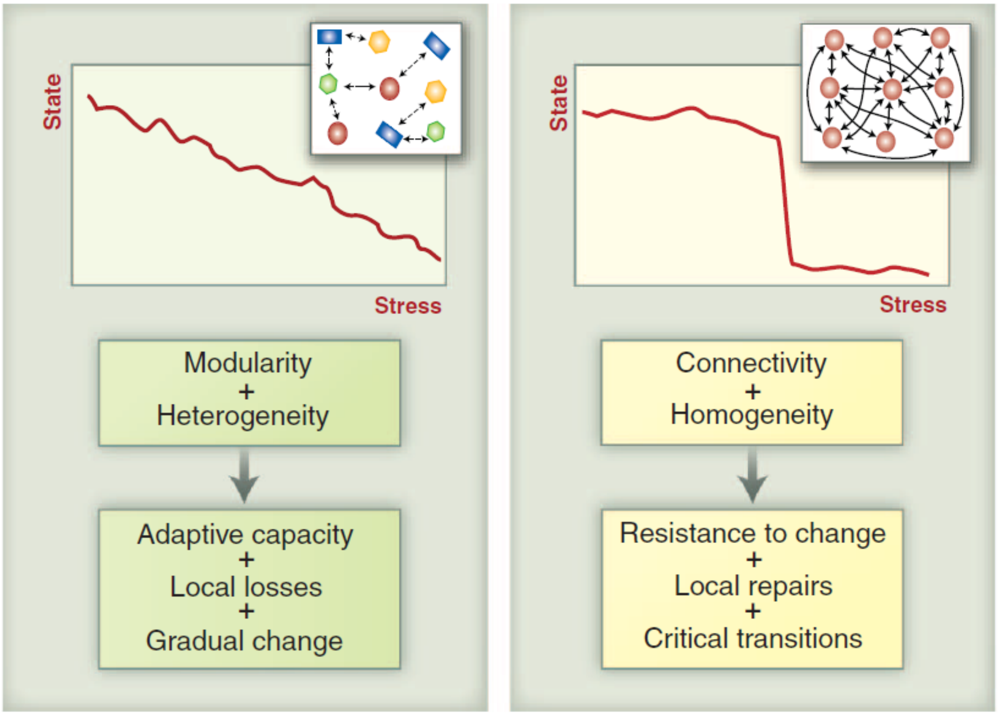

Figure 1: [3] Here we note two important factors in whether or not a critical transition occurs.

3 Modelling + Simulations

Practically speaking, in the ecological sense there are issues of scale when creating an experiment to investigate the critical regime. Ecosystems such as fisheries are globally connected phenomena which, although data can be collected, are not experiments, per se, because scientists did not set up the system nor control its parameters. These situations result in data modelling, from which simulation of such data naturally follows.

In Scheffer's paper, he notes that catastrophic bifurcations can be called "tipping points". We examine an attempt by Biggs, et al. [5] to model a fisheries food web impacted by human development. The details of this model and the simulation of such an ecosystem are not important, but a general picture is given in figure 2. What are important are the indicators derived that provide a warning before a critical transition. Notably, these simulations

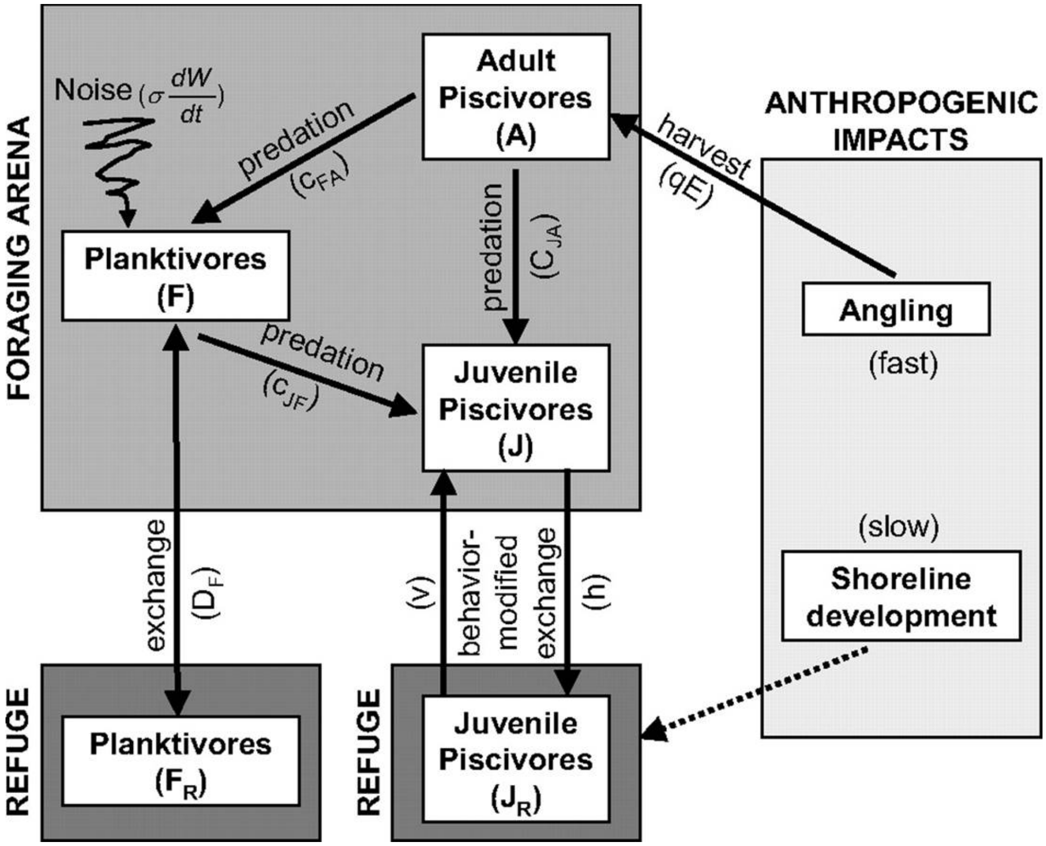

Figure 2: From [5], a model of a fisheries food web and the impacts of the included factors.

provide a timescale expected under the input conditions over which we can expect to find such indicators. Biggs notes that concepts such as variance, skewness, kurtosis, and others give an indication of critical behavior but only once that behavior has begun and they depended on other conditions such as high levels of environmental noise in their model. Nevertheless they found that when a 10 year spectral density ratio exceeds 1 that there is an impending critical transition. This is significant because it allows, from a modelling of data, a way to look out for signals of critical transitions ahead of time in real systems, where collapse is irreversible and not merely a function of reprogramming. See also, Veraart et al [6].

4 Experiments

In many physical systems, the scientist can actively and controllably tune the parameter near the critical region. In some systems, such as superconductors, the critical region is comparatively narrow, resulting in an inability to experimentally see the critical behavior. In other systems, the issue is repeatability, where the system is something beyond the experimenter's control, as we saw before. The challenge then is to both increase the system size and complexity while maintaining control of its parameters, and in this way examine the nature of the critical transitions. This is perhaps the highlight of the field currently, as it best links the understanding of the theory to the complexity of the modelling.

4.1 Yeast Colonies

We take as our example here studies on yeast colonies done by Dai, et al. in Dr. Jeff Gore's lab at MIT [7]. First, experiments were done on the effect of population dilution on recovery of such populations under the effect of salt shock. Specifically, yeast colonies were grown, then diluted, then allowed to grow again. These populations were then introduced to some perturbation (the salt shock), and their population monitored. Populations with low dilution endured the shocks, while populations with high dilutions collapsed. Here we can see two important aspects of this experiment that have been observed: bistability, as expected from theory, and the Allee effect, as observed in ecological systems. [8]

Bistability seems simple enough: two stable states, with a phase transition between them. However the fact that there are just these two states should be notable. When dilution rates were in the intermediate regime, the Dai team found that the yeast colonies diverged to one the stable population states after the action of the external salt shock. Importantly, colonies which began closer to a stable state maintained that state under such a shock. Thus the MIT team was able to control a critical transition in the population density of a yeast colony by dilution, as seen in figure 3.

4.2 Yeast "Cheaters"

A newer effort [9] in the same area by the same group demonstrates the power of these methods. A. Sanchez, in the Gore group, altered the DNA of

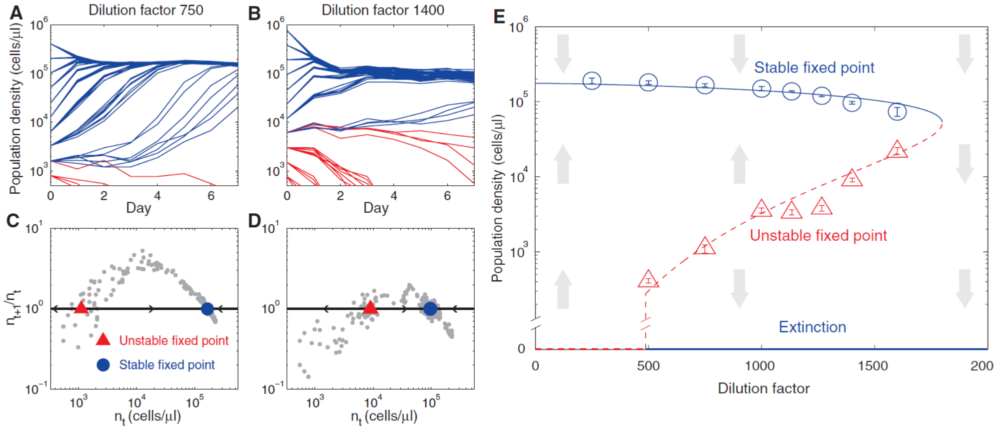

Figure 3: From [7], on the left (A-D) we can see that for a variety of initial population densities, the system becomes bistable, tending towards one of two fixed points. On the right (E), we can see a fold bifurcation diagram from actual yeast colony data. Here, the lower "stable" state is extinction.

some of the yeast to not hydrolize the sucrose necessary for the survival of the yeast colonies. These they termed "cheaters", and they tested the effect of varying the fraction of cheaters within the population on the stability and survivability of the system. The change in DNA is an important feature in this experiment. In most real world systems, the individuals can react and adapt somewhat to the changes in their ecosystem on a time scale that is comparable to that of the change. By encoding the behavior of the yeast in its DNA the experimenters forced the yeast to choose one stratgy for its lifetime. Hence cheaters (and their descendents) will be cheaters, and cooperators will be cooperators. This simplification creates another tunable parameter, and thus they were able to plot the fixed points of the system in population density / cheater fraction space, as seen in figure 4 A.

5 Conclusions

Finally, I'd like to conclude with another figure from Scheffer (figure 5 [3]), which really focuses on the recovery and policy aspects of these critical transitions. After all, these real systems are very real, they are much more than

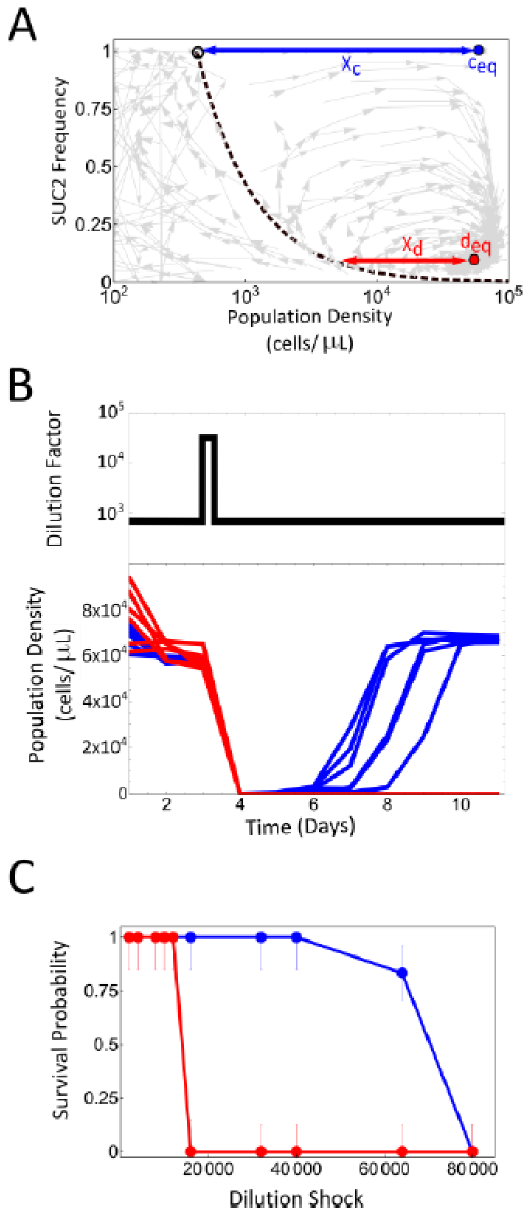

Figure 4: Data from a mixed population of yeast cheaters and cooperators [9]. A shows the fixed points and flows in the parameter space of cheater fraction vs. population density. From B, we can see that the cultures with high cooperator fractions recover(blue), while the high cheater fraction do not (red). From C, we can see that high cooperator fractions can endure much higher dilution shocks (blue) than those with high cheater fractions (red).

a mathematical or scientific experiment, and they affect the course of civilization. We have seen several examples of critical transitions in ecology, and the motivations behind creating a theory thereof. Predicting the behavior of collapsing systems on an ecological scale is a lofty goal, coupling theory, modeling, and experiment to tangible policy and programs to mitigate ecological collapse at the hands of human impacts such as pollution, deforestation, and overfishing. The situation is, as we have seen, that many of these systems exhibit bistability, and that in the view of conserving renewable natural resources, it is far preferable to maintain the high levels of population densities (or health of the population). Furthermore in the same view it is preferable to have fast recovery times, so that resources may be extracted at a high rate while that resource is able to recover. So, keeping these renewable resources out of the critical regime avoids two dangers. The real danger, however, is the fact that critical transitions in real systems are irreversible. This means that there will not be a rapid population increase like there would be a massive die-off, at least given the fact that the demand for this resource will not have abated, so the pressures which caused the population to crash will continue to act on the lower stable state.

So, we will conclude here by noting that the economy and ecology, while good analogies, are not independent. While natural cycles of population booms and busts occur, certainly one of the biggest impacts on ecosystems globally is the rise of the human ecosystem: the economy. Modern economy has enabled the largest impacts on the ecology of the world, on par with global events such as meteor strikes, with similar patterns of massive extinction and ecological change. I will speculate that the portion of the ecosystems in the world which are unaffected by human action is vanishingly small. Even over the frozen abyss of Antarctica, humans have opened a hole in the ozone layer. Perhaps there is some cave pool ecosystem in some undiscovered cave, continuing in its darkness as it has for millennia, which has escaped the reach of humanity. However, unlike the meteor strike, humanity persists, and so, even for the cave pool, it may only be a matter of time.

References

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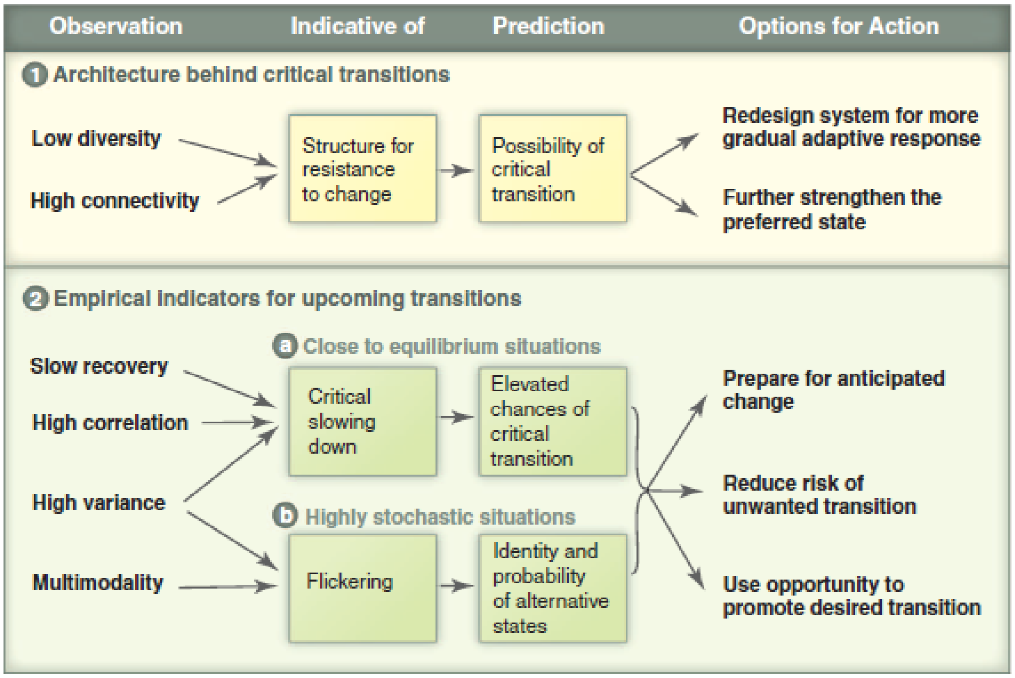

Figure 5: [3] Different classes of generic observations that can be used to indicate the potential for critical transitions in a complex system.

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