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Math 53: Chaos!

Resilience and Regime Change in Ecosystems: Bifurcation and Perturbation Analysis

Background

"Resilience Thinking" is a new paradigm of Sustainability and Environmental Science. It refers to a unified way of conceptualizing and managing social-ecological systems. The goal of managing for resilience is to maintain the ability of a system to absorb stochastic and human-generated perturbations and return to the current state. If the system is improperly managed and resilience decreases, the likelihood of a regime change, where the system crosses a threshold to an alternate stable state, is increased. We know that certain aspects of a system, including diversity, redundancy, hierarchy and self-organization, tend to increase resilience independently of the actual structure of the system.

Resilience Thinking, as a paradigm, has a lot to offer without further mathematical development, but whether further mathematical exploration has much to offer ecology is an open question. Many ecologists believe that mathematical models are much too simplified to be applied to real ecosystems. Additionally, the amount of unpredictable, stochastic forcing in real ecosystems is an obstacle for any deterministic theory of ecology (Schaffer 1985).

In this paper I will present a small set of practical mathematical tools that can be applied to resilience management, including detecting regime thresholds, analyzing system reactivity to understand local perturbation responses, and better understanding chaotic regimes and bifurcations.

Evolution favors stable, resilient systems not liable to catastrophic regime changes or chaotic behavior (Berryman and Millstein 1989). Even if a system exhibits transient chaos it tends to return to a stable state (Upadhyay 2009). Instead, these behaviors often result from human intervention, and that is where these tools will be most useful. This is not a great limitation because the basic assumption of resilience thinking is that systems are most resilient in their natural (evolved states), so we would like to understand how human intervention affects natural systems.

Models

The basic model of continuous-generation species growth is the differential equation system (1) due to Lotka and Volterra independently in 1925 and 1926. It is a predator-prey model where the growth of species x is limited by predation by species y, and the growth of species y is limited by availability of prey x. This model has limitations, and represents a simplistic Holling-Type I Functional Response, which does not model saturation of prey (i.e. prey consumption remains proportional to prey

density until the maximum is reached). The model that I will focus on is a prey, predator and top-predator model with a Holling-Type II functional response (equation 2), where prey consumption slows with respect to prey density near the maximum.

$$\frac{dx}{dt} = x(\alpha - \beta y)$$
$$\frac{dy}{dt} = -y(\gamma - \delta x) \tag{1}$$

$$dx/dt = x(1 - x) - f_1(x)y$$
$$dy/dt = f_1(x)y - f_2(y)z - d_1 y \tag{2}$$
$$dz/dt = f_2(y)z - d_2 z$$

$$f_i(u) = a_i u/(1 + b_i u).$$

The dynamics of the predator-prey Lotka-Volterra Model are simple and the stabilities of the fixed points can be easily determined from the parameters. As you increase the number of species in this model, the possible behaviors become more complex including periodic orbits and limit-cycles in three dimensions and chaos in four (May and Warren 1975).

The Holling-Type II model is more realistic in its behavior and the nonlinearities produce chaos in only three species, which is easier to visualize. The three-species chain is also considered a food-web "unit", because food webs can be composed of smaller chains, so understanding the dynamics of the chain will hopefully help us understand larger systems.

Detecting Thresholds

Approaching a threshold between alternate stable states in a system leads to a phenomenon called "critical slowing down," where system indicators change more and more slowly. This can be detected by the presence of lower frequencies in the data.
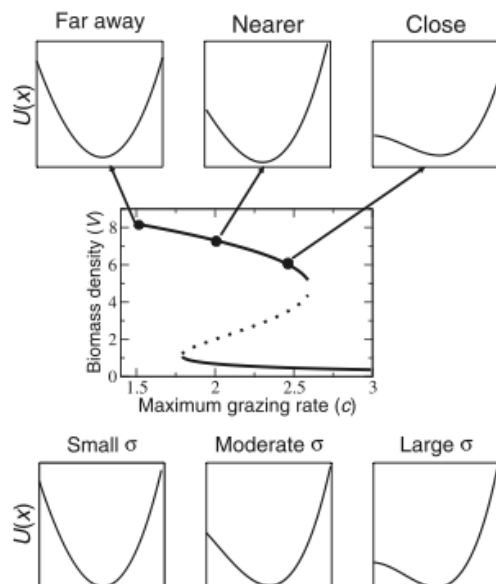

Figure 1: Structure of the local potential function near a threshold. (Guttal and Jayaprakesh 2008)

Additionally, the local potential function becomes more asymmetrical near a threshold, because a threshold is a leveling-off of the potential (figure 1). This can be detected in the data as well, because a small perturbation is more likely to skew the data farther in one direction because the potential is flatter, which leads to increased variance and skewness (Andersen et al. 2008).

Reactivity and Perturbations

When a system is near a threshold, it is valuable to have some understanding how it will react to perturbations, either internal or external (stochastic). Reactivity can refer to a variety of ways of measuring the short-term reaction of the system, including the maximum rate of change immediately after a perturbation, the maximum deviation from the stable state before returning, or the *perturbation envelope*, the curve consisting of the maximum deviation at each time step after the perturbation (figure 2) (Neubert and Caswell 1996).
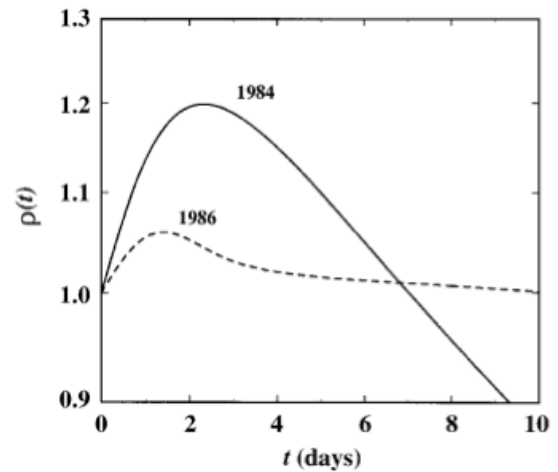
Figure 2: Perturbation envelopes for a lake ecosystem in 1984 and 1986.

Two matrices with the same stability (and eigenvalues) can react differently in the short term (although they will act the same in the long term). This short-term reactivity can be analyzed by calculating the eigenvalues of the symmetric (Hermitian) part of the matrix. To compute these values, we can linearize the ecosystem model at a typical point or construct a complete linear model. The compartment model, a matrix whose entries represent resource flow between ecosystem "compartments, " is an example of a linear model that can be generalized to most ecosystems.

Neubert and Caswell (1996) calculated the reactivity of a lake ecosystem compartment model published by Carpenter et al. in 1992. They found that the reactivity was significantly decreased by the addition of a top-predator (a large fish) to the ecosystem (the top-predator was added between 1984 and 1986). This confirms the intuition that a top-predator will tend to damp large fluctuations. There data also confirmed that a longer food chain takes longer to return to the stable state, because perturbations propagate further (figure 2).

Bifurcation Behavior

A bifurcation diagram of the Holling-Type II equations for different values of parameter b_1 (figure 3) shows that chaotic regimes exist for many values greater than 2.4. For some values of b_1 (e.g. 2.47), there are simultaneously stable periodic orbits and chaotic orbits, depending on initial conditions. A perturbation test on a stable initial

Figure 3: A bifurcation diagram of the Holling-Type II equations (2) for different values of parameter b_1 plotted agains the maxima of species z.

condition for $b_1 = 2.47$ shows little correlation between the amount of the perturbation and the behavior of the orbit. In other words, the attracting regime is unpredictable at these parameter values and resilience management is more sensitive and thus more imperative. Chaotic regimes are undesirable from a management perspective and also because chaos, which induces large swings in population, increases the chances of a deterministic species extinction (i.e. one not caused by stochastic fluctuations) (Berryman and Millstein 1989).

  Catastrophic (sudden and discontinuous) regime changes are not unusual in nature and can be devastating, even if the switch is between two stable states. Examples include desertification, algae-dominated coral reefs, lake eutrophication and many others that may be induced by climate change. These are all situations where the balancing feedback mechanism of the system is overwhelmed, often by human inputs, and reinforcing feedback takes over suddenly.

  A catastrophic switch that cannot be reversed by simply returning inputs to prior levels is

Figure 4: Hysteresis in lake eutrophication.

called *hysteresis*. Hysteresis occurs when there is a fold in the state space of the system, so that there are two possible states for one set of conditions. In this case, changing the conditions and external forcing can both cause the system to jump from one stable state to the other (figure 1). Figure 4 shows this situation in a lake-eutrophication model.

  Bifurcations in flows are defined on Poincaré Maps, which means that a stable point can represent a stable periodic orbit depending on the cross-section. If a system adds one or more dimensions of periodicity, that is reflected in an appropriate Poincaré Map as a switch from a stable point to a periodic orbit. This switch is called a Hopf bifurcation. A Hopf bifurcation is when a path of stable equilibria is replaced by a periodic orbit or limit cycle (on a Poincaré Map). This is a common behavior in ecosystems, which are naturally periodic. Higher amplitudes of fluctuation make the system less stable; conversely, a cessation of periodicity can signify an extinction.

  Muratori and Rinaldi (1989) analyzed the Hopf bifurcation behavior of the three-species system in equation 2. They analyzed the system using graphical methods and Jacobian calculation using constant levels of the top-predator. This generated a
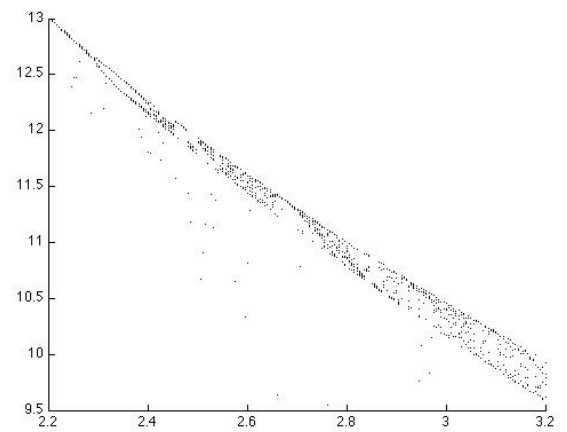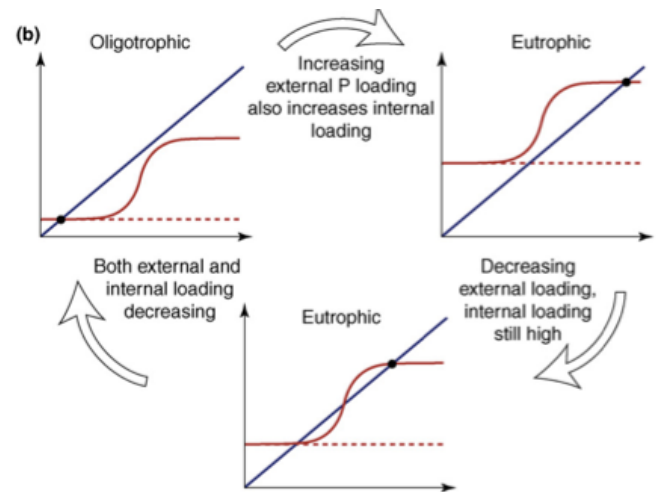
bifurcation diagram with the level of the top-predator as the key parameter. This is useful because top-predators are more measurable and more measurably affected by human action. For example, in Schaffer (1985) and Gamarra and Solé (2000), bifurcation analysis suggests that lynx-trapping by humans caused chaotic amplitudes observed in the Canadian lynx cycle of the 19th-century. In this case, the Poincaré Map switched from a single stable point to a chaotic periodic attractor (figure 5).

Rinaldi and Muratori used isoclines (x',y' = 0) to determine the behavior of the system at different levels of the top-predator. Changing this constant shifts only the y' isocline in a predictable way. Different isocline shapes and intersections produce different bifurcation types. Figure 6 shows the possible intersections. If the isoclines
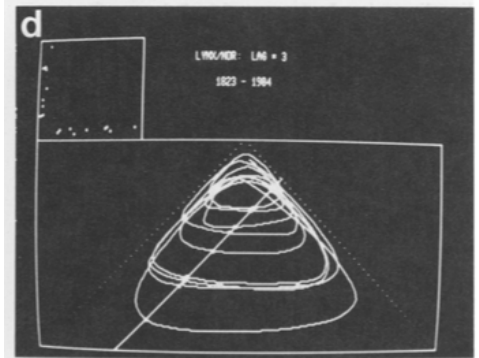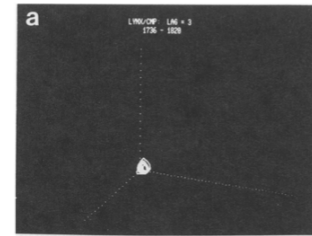

Figure 5: Switch from stable equilibrium to a chaotic periodic attractor in the 19th-century Canadian lynx cycle.
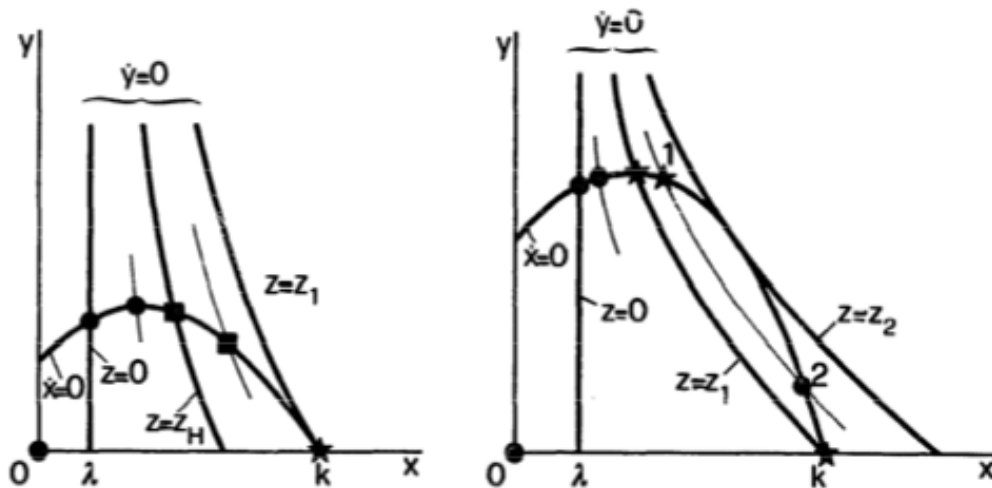

Figure 6: Isoclines of the prey, predator, top-predator model.

behave as on the left, then the bifurcation behavior is smooth. The stable co-existence equilibrium bifurcates smoothly from the x-only equilibrium, and then bifurcates into periodic cycles of x and y (at z_H, where the equilibrium goes unstable). Because these are smooth transitions, they can be reversed simply by returning the z-population to prior levels. The situation on the right leads to catastrophic regime switches (hysteresis). It either introduces a catastrophic bifurcation of stable states (called a saddle-node bifurcation) or a catastrophic Hopf bifurcation, where the system jumps from stable periodic orbits to extinction of y (and therefore z) (figure 7). Which situation occurs depends on the stability of the intersection labeled (1) in figure 6, which controls where the Hopf bifurcation (z_H) occurs.
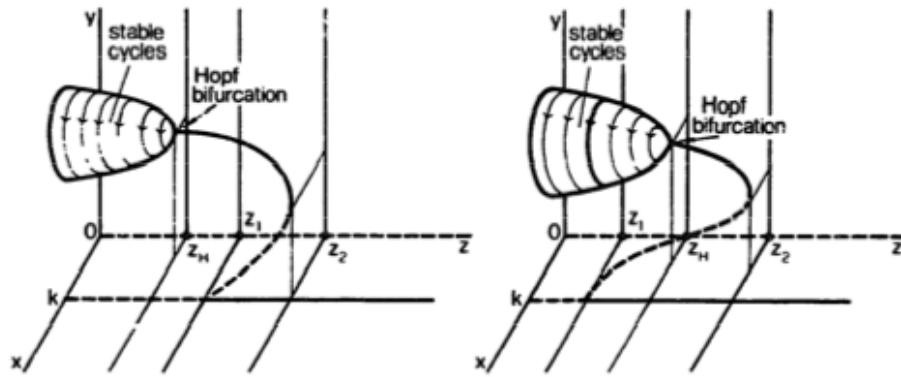
Figure 7: Allowed bifurcations of figure 6.

Conclusion

The promise of resilience thinking is an actionable set of rules and management practices based on a broad understanding of ecosystems. It does not require the precise understanding that were needed for previous paradigms of ecosystem *control*, a notion that has been all but abandoned after many catastrophic failures. The mathematics of chaos promised in its earlier years (e.g. Schaffer 1985) to contribute to a precise, deterministic model, but that idea has since faded. Instead, contributions have paralleled the shift to resilience thinking, offering a broader understanding of possible system behaviors and the effects of human intervention. Recent papers by Liu and Chen (2002) and Zhang and Chen (2004) study the effect of impulsive perturbations on the system I explored and find that increasing the amplitude of these perturbations predictably increasing the amplitude of the resulting chaotic fluctuations. I believe that, while chaos may not offer the precise understanding once sought, it does have a lot to offer ecologists and policy-makers in a time of increasing pressure on ecosystems.

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