Resilience in Biological Systems: Classifying the Stability of Flow-kick Equilibria Alanna Haslam, Class of 2020

In recent years, the scientific community has become increasingly alarmed by current and projected reports of rapid climate change. Global warming, rising sea levels, melting ice caps, and increased frequency of extreme weather events threaten ecosystems which we are reliant on both for resources and for the sustained biodiversity of the planet.¹ In light of these growing concerns, scientists are needing to ask more questions about the resilience of these ecosystems to environmental disturbances. Among these questions are those which address how sustainable management techniques might be used to maintain the desired stable states of ecosystems.

To simulate these scenarios and the ways that management techniques might influence them, we turn to mathematical modeling. In particular, we use flow-kick dynamical systems to model periodically managed ecosystems and quantify their resilience to environmental change and management strategies. Flow-kick systems consist of repeated periods of undisturbed, natural growth (flow), each followed by a discrete intervention (kick) (see Figure 1).²



Figure 1. Visualization of a flow-kick dynamical system. The image on the left shows two iterations of flow and kick. The image on the right shows how the behavior of this flow-kick system settles after many iterations.

Flow-kick systems provide a mathematical framework for answering questions such as: *How will this management strategy affect the long term stable state of the system? How resilient would the system be to disturbances in a chosen management strategy?* Techniques for using flow-kick systems to answer these questions have been developed in one dimension.³ In higher dimensions, however, researchers are

currently reliant on computational models and simulations. Though simulations are important and useful, they take time to build and are often computationally expensive.

With the general goal to extend analytic understanding of flow-kick systems in higher dimensions, I spent the summer deepening my understanding of previously developed techniques for analyzing the stability of flow-kick equilibria. In particular, I studied the variational equation which pieces together linear approximations of local behavior to determine the tendencies of the system nearby equilibrium solutions.⁴ This led me to think critically about situations in which viewing the variational equation as a series of linear approximations leads to incorrect intuition. In turn, I began to study what mathematical conditions allow for this intuitive process to work and which require us to seek more information (see Figure 2). This work culminated in proving a theorem about the classification of flow-kick equilibria which satisfy a certain set of conditions.



Figure 2. The mathematical conditions which I was examining relates to the region of state space in which the equilibrium trajectory is located. It is around the points on this trajectory that the approximations of the variational equation are built. The result I developed over the summer relates to the "non-reactive attractor" region in white. This semester I was working on developing techniques to understand the "reactive attractor" region in blue.

This semester my work has focused on exploring those particular circumstances in which our classical approach to the variational equation may fail. The reason for this failing has to do with the distinction between transient and asymptotic behavior (see Figure 3). By thinking critically about this distinction and the quantitative indicator of it, reactivity,⁵ I was able to construct an example of when

our intuitive hypothesis about the behavior of the variational equation is the reverse of its actual behavior. From this example, I started to think about how to analytically characterize the accumulation of transient behavior, and how to easily determine when this cumulative behavior can or cannot go against our intuition.



Figure 3. Both of the above images depict the behavior of a system which asymptotically approaches the origin. These two images, however, display different transient behavior. The system on the left sometimes has transient behavior which takes solution curves further away from the origin. The system on the right always, for all periods of time, takes solutions closer and closer to the origin.

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