Early-Warning Signals Predictors of Extinction Events in Dynamical Models

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Abstract

We consider an SIS (susceptible-infected-susceptible) epidemic model, as well as a density-dependent population model (Allee effect). Using Monte Carlo methods, we simulate stochastic data and subject it to analysis using metric based indicators developed in the theory of Early-Warning Signals. The analysis presents important information about the resilience to perturbations of simulated time series, which is then employed to apply control measures to affect the behavior of the models. We show metric based indicators can be used to favorably induce early extinction events in the aforementioned models. We also expose the dangers of the application of control measures when the system is in a highly resilient state, underlining the importance of extraction of information from a system before attempting to affect its behavior through quarantine and/or vaccination measures.

Keywords: early-warning signals, critical transition, control measures, epidemic, extinction, Allee effect.

1. Introduction

Recent events concerning the outbreak of infectious diseases such as Ebola and Zika have brought to light the need to develop effective and integrated measures to both monitor and control the spread of epidemics, in order to stop regional outbreaks from potentially becoming international crises and to mitigate the damage done to the affected areas. In a similar vein, climate change and its effects on coral reefs, animal populations and grasslands, has accentuated the importance of the study of tipping points in ecological systems and its effects on their overall resilience to underlying drivers.

Previous approaches to these problems include the study of the theory of Early-Warning Signals (EWS) to detect critical transitions in progress, mainly as a prediction tool for stochastic switching in disease emergence and ecological tipping points[7, 8]. Research in this area suggests that stochastic switching can be anticipated if data is collected with sufficient frequency [7].

This, however, has proven difficult in practice given that, for instance, disease emergence is characterized by low prevalence and is oftentimes complicated by amplification of transients and oscillatory dynamics [8]. Also, it is widely held that stochastic switching cannot be detected since there is no change in the shape of the potential function, and no change in the eigenvalue of the mean field model [7, 19]. Furthermore, insights from large deviation theory cast doubt on the effectiveness, accuracy, and feasibility of said approach [11, 12, 13].

Nevertheless, extensive research shows that generic early-warning signals exist in a wide variety of systems, and can in fact be the harbingers of critical transitions [16, 17]. For instance, the presence of leading indicators such as auto-correlation and variance have been found to increase prior to past climatic transitions, and regime changes in lake food webs [5, 6, 18, 19]. And although, as previously stated, the early detection of a stochastic regime switch i.e. a critical transition is difficult to predict by sole reliance on the generic indicators developed in the theory of EWS, the changes detected by said indicators do tell us that some type of transition is taking place, be it critical or otherwise [14]. This observation will serve as the foundation of our research, as we seek to test and develop methods that introduce control measures at critical stages in the dynamics of the models under study.

In order to circumvent the difficulties and controversies previously outlined, in our work we seek to pursue a different approach, namely, to employ the metric-based indicators developed in the theory of EWS to monitor the state of the system thereby ascertaining its overall resilience to control measures at different points in time. We seek to drive these systems to early extinction by perturbing them at specific points corresponding to states of low resilience i.e. weakened system state. Similar experiments have been carried out by Dai et al. albeit with a different goal in mind, where of loss of resilience is defined as the distance between stable and unstable manifolds [3]

In short, whereas previous attempts focused on the prediction of critical transitions in stochastic systems, we attempt to induce them. We hypothesize that perturbing the system while in a weakened state will precipitate critical transitions, while the same approach applied during periods of increased resilience will be met with resistance, failing to yield similar results. Our hypothesis stems from results that show that many stochastic systems do in fact behave like systems undergoing critical transition due to CSD in the mean field model [7].

We test our hypothesis by simulating stochastic data from dynamical models using Monte Carlo methods. With the data in time-series form, we subject it to analysis using the **earlywarnings** package in R [4, 5, 6]. Metric-based statistical indicators such as auto correlation, return rate, skewness, and variance yield actionable information which is then used to introduce quarantine/immunization/harvesting measures to effect the desired result.

Consistent with our proposition, we show that pulsing the infected population in the SIS model at the low-resilience state by quarantining/immunizing a portion of the population is an effective measure for inducing early extinction events in the epidemic. Mean extinction times (MTE) are computed for the various cases and compared, showing agreement with our hypothesis. Results also warn against the indiscriminate application of controls when the system is in a high-resilience state.

Last, all of the results obtained in the SIS model are duplicated in similar fashion in the population model with Allee effect, where the focus is to induce an early extinction event in a pest population by extracting/harvesting a portion of the population.

2. Theory

Early-Warning Signals can be thought of as the direct product of the need to understand the phenomenon of critical transitions. Said phenomenon corresponds to catastrophic bifurcations, in which the qualitative behavior of the system changes abruptly in response to changes in one or more external parameters. It commonly arises in systems with alternative states such as endemic/extinct states in epidemic models, or stable/unstable states in population models.

In addition, critical transitions exhibit “threshold behavior”, which is accompanied by changes in the system properties that become more extreme as it moves closer to the tipping point. These changes include but are not

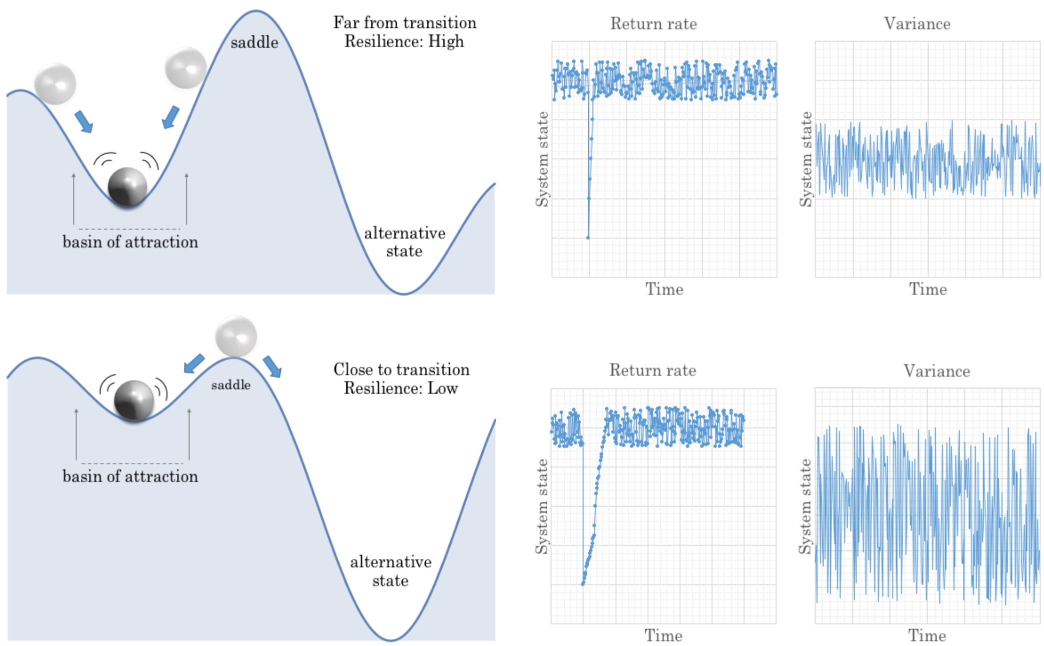

Figure 1: **Top left:** dynamical landscape far from the transition. Deep basin of attraction makes switch to alternative state due to small perturbations difficult. **Top right:** far from the transition, return rate is fast, variance is relatively small.
Bottom left: flattening of the dynamical landscape due to critical slowing-down can cause even small perturbations to induce a switch to an alternative state. **Bottom right:** close to the transition, return rate slows down, variance increases.

limited to: increasing auto-correlation, decreased return rate, increasing variance, increasing skewness, and flickering [2, 9].

The gradual change in these collective properties is generally termed "critical slowing-down" (CSD). In essence, it is CSD that allows Early-Warning Signals to detect critical transitions in progress, and it is precisely the careful monitoring of these metric indicators that will serve as the basis for our analysis. Figure 1 illustrates the behavior.

One thing we'd like to point out is that while CSD is typically associated with undesirable outcomes in the systems undergoing these changes (such as desertification, lake eutrophication, coral reef collapse, etc.), in our work we seek to take advantage of the resulting dynamics consequence of CSD so that we may accelerate critical transitions in systems where such outcomes are indeed desirable, such as the extermination of pest populations, and the local extinction of epidemics.

With basic theory and terminology out of the way, we move forward to simulate data from select dynamical models so that we may test our hypothesis against EWS theory.

3. SIS Epidemic Model

We begin by considering a simple SIS epidemic model. Individuals are born into the susceptible population S at the rate μN, and once in this compartment they can perish at rate μS or become infected, moving to the respective compartment at rate $\beta SI/N$, where N represents the total population number, μ (1/year) the birth/death rate, and β (1/year) the contact rate.

In the infected compartment I, individuals can recover at rate γI, or perish at rate μI. Here, γ (1/year) represents the recovery rate, and μ is as before. Figure 2 illustrates the dynamics.

In order to keep our analysis as simple as possible we opted to keep the population number N constant, which led to our decision to make μ serve dual purpose as birth and death rate.

Mathematically, the model is expressed by the following system of ODEs:

$$\frac{dS}{dt} = \frac{-\beta SI}{N} + \mu(N - S) + \gamma I, \tag{1}$$

$$\frac{dI}{dt} = \frac{\beta SI}{N} - \mu I - \gamma I. \tag{2}$$

The steady states for this system are given by:

$$(N, 0) \longrightarrow \text{disease free}, \tag{3}$$

$$\left(\frac{N}{R_0}, N\left(1 - \frac{1}{R_0}\right)\right) \longrightarrow \text{endemic}, \tag{4}$$

where $R_0 = \frac{\beta}{\gamma+\mu}$, is defined as the reproductive number [1].

The corresponding transitions and associated rates are given by:

Transition	Rates	Event
$S, I \xrightarrow{\mu} \varnothing$	$\mu S, \mu I$	death
$S \xrightarrow{\mu} 2S$	μN	birth
$S \xrightarrow{\gamma} 2S$	γI	recovery
$2I \xrightarrow{\gamma} I$	γI	recovery
$I \xrightarrow{\beta} 2I$	$\dfrac{\beta S I}{N}$	infection
$2S \xrightarrow{\beta} S$	$\dfrac{\beta S I}{N}$	infection

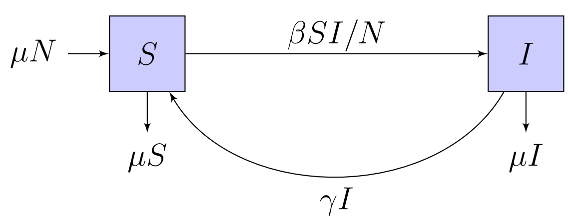

Figure 2: SIS compartmental diagram.

4. Population model with Allee effect

In order to test the effectiveness of EWS as a monitoring tool across various systems, we extend our hypothesis to include a density dependent population model with Allee effect.

Mathematically, the system is given by the following ODE:

$$\frac{dX}{dt} = \frac{-\sigma}{6} X^3 + \frac{\lambda}{2} X^2 - \mu X, \tag{5}$$

where σ represents the death rate due to overcrowding, λ represents the optimal-density growth rate, and μ represents the low-density death rate [15].

The corresponding transitions and associated rates are given by:

Transition	Rates
$X \xrightarrow{\mu} \varnothing$	$\mu X,$
$2X \xrightarrow{\lambda/K} 3X$	$\lambda \dfrac{X(X-1)}{2K}$
$3X \xrightarrow{\sigma/K^2} 2X$	$\sigma \dfrac{X(X-1)(X-2)}{6K^2},$

where K stands for the population carrying capacity.

The stable steady states are given as follows:

$$X_1 = \frac{K(3\lambda + \sqrt{9\lambda^2 - 24\sigma\mu})}{2\sigma} \qquad \longrightarrow \text{stable} \tag{6}$$

$$X_2 = \frac{K(3\lambda - \sqrt{9\lambda^2 - 24\sigma\mu})}{2\sigma} \qquad \longrightarrow \text{unstable} \tag{7}$$

As with the SIS model before, the population model with Allee is subjected to stochastic simulation, which is where we focus our attention next.

5. Simulation

Stochastic simulation of data from the models introduced previously is accomplished by adapting Gillespie's Algorithm to our purposes. The algorithm is a form of dynamic Monte Carlo method originally designed for the simulation of reaction-diffusion type interactions between molecules in chemical and biochemical applications [10]. The algorithm is implemented in MATLAB®, and the steps are as follows:

1. Initialize all variables and parameters: set population size, as well as birth, death, and contact rates.

2. Draw two random numbers: first number determines which event takes place, while the second one determines when the event takes place.

3. Update populations and time step: depending on the event determined by the random numbers, add/subtract individuals to reflect change. Move time forward.

4. Repeat: continue iterating through steps 2 and 3 until extinction is reached (in the case of SIS and population model) or until max. number if iterations is reached.

As an example, for the SIS model, a random number coinciding with $\frac{-\beta SI}{N}$ would indicate an infection event in the susceptible population, warranting removal of one individual from the S compartment, and moving it into the I compartment.

The simulated data is then put into time-series form taking care to store the population values in equally spaced time intervals. This greatly simplifies the manipulation of data, as well as subsequent analysis.

6. EWS Analysis in the R environment

In order to be achieve the results outlined in our hypothesis, we must first analyze the simulated data by running it through the **earlywarnings** package developed by Vasilis Dakos and Leo Lahti for R. As stated by its developers, the toolbox provides methods for estimating statistical changes in timeseries that can be used for identifying nearby critical transitions [4, 5].

While the Early-Warning Signals toolbox contains robust methods to analyze time-series using both model-based (ARMA, GARCH, AR(n)) and metric-based indicators, in our work we seek to rely only on the latter as this provides us with more flexibility in the application of the theory across various dynamical systems.

After importing the time-series data into R, we pass it into the **generic_ews** method in the toolbox. The resulting output is shown in figure 3.

From our earlier discussion of EWS theory, we know that the statistics when we're far from the transition are very different from when we're close to the transition. This is reflected by the rise in auto-correlation, variance, and skewness, and inversely by a drop in the return rate. It is precisely at this point where we introduce control measures such as quarantines/vaccines in the SIS model, and partial removal of the population in the Allee model.

As one may observe from figure 3, it is possible for these indicators to signal a critical transition in progress, while failing to switch to an alternative state i.e. a false positive. However, by pulsing the system at the right time,

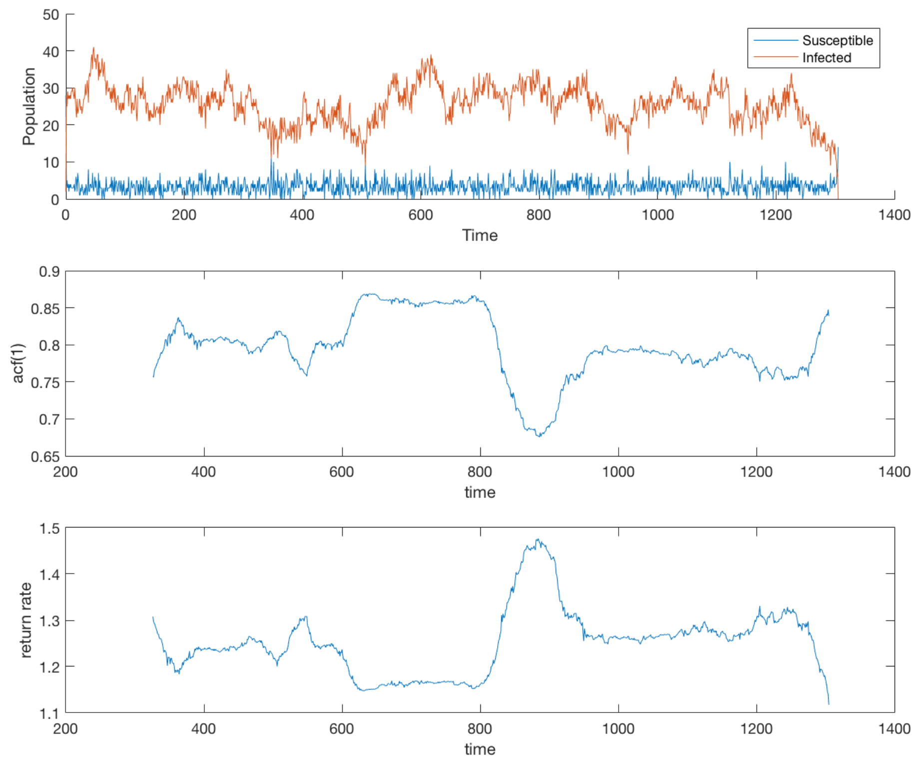

Figure 3: output from the **earlywarnings** package in R plotted in MATLAB. Statistical metric-based indicators give us an accurate picture of the state of the system (SIS model).

we can precipitate the transition and achieve early extinction events. This loss of resilience is a trademark of CSD.

As we shall see, the results obtained by relying on metric-based EWS analysis are both encouraging and sobering.

7. Statistical Thresholds

Since our methods call for the introduction of control measures when the system is displaying threshold values in auto-correlation (high/low), it is essential that we define specifically what these thresholds are and the manner in which they were obtained. We note that at this point, we take auto-correlation as our leading metric indicator in the analysis and simulations that follow.

In order to ensure robust statistical estimates, one thousand iterations of each model were produced and subjected through EWS analysis in R. The auto-correlation data points of each of the one thousand iterations was averaged out to obtain a mean auto-correlation specific to the time-series in hand. In turn, these one thousand means were averaged out to obtain a clearer idea of the distribution and location of the thresholds that would indicate the high/low auto-correlation points.

The results are summarized in table 1 and figure 4. These numbers present us with a metric by which to determine how far we're willing to let the system run in our simulations before the application of control measures.

Table 1: statistical thresholds (auto correlation)

threshold type	SIS	Allee
high	0.90713	0.85536
low	0.71253	0.51336

Thus, in all of our simulations we introduced vaccination/quarantine measures in the SIS model whenever the auto-correlation reached or surpassed the aforementioned values for high/low. The results were then compared and checked for agreement against our hypothesis. Similarly for the model with Allee effect.

8. Results and Discussion

SIS Model

The model outlined in section 3 is implemented in MATLAB® with parameters given by: $\mu = 0.02$, $\beta = 1000$, $\gamma = 99.98$. The resulting value for the reproductive number $R_0 = 10$. The population size N is varied as needed. Lastly, the simulation was carried out for 10^7 iterations.

As figure 5 illustrates, pulsing the infected population at the low-resilience state corresponding to high auto-correlation, variance, skewness, and decrease in return rate suffices to induce a critical transition to its alternative, extinct state.

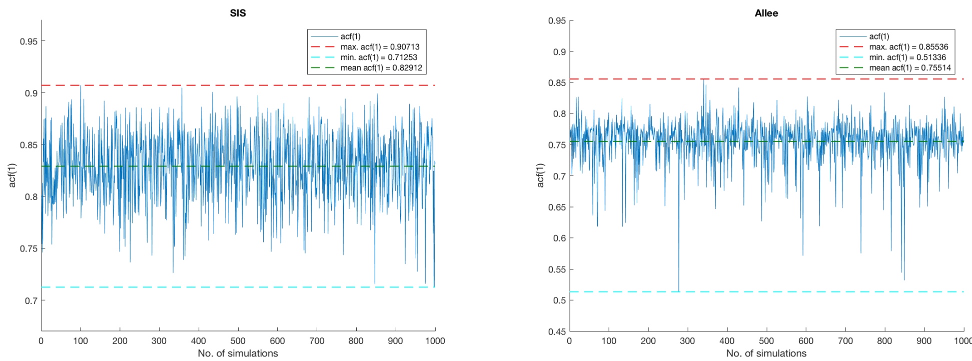

Figure 4: auto-correlation analysis for one thousand runs of the SIS and Allee models.

However, consistent with our hypothesis, quarantining individuals at the high-resilience state (low auto-correlation, high return rate) fails to precipitate an early extinction event. Original, unperturbed time-series is presented along with the results for comparison.

It is important to point out that in order to ensure unbiased results, all control measures were introduced when the population sizes in the high/low resilience states were virtually the same. Similarly, the amount of individuals quarantined was kept exactly the same.

As we can see, these results are encouraging since we've shown that by monitoring the system and attacking it with conventional control measures can lead to a significant reduction in the active cycle of the epidemic. Nevertheless, this approach needs to be employed with care.

For instance, the results presented in figure 6 paint a perplexing picture. Consistent with the case examined previously, the quarantining/immunization of infected individuals during weakened system states drives it to early extinction. However, pulsing the system at the high-resilience state exacerbates adverse conditions, ultimately causing an extension of the life cycle of the epidemic. This is at the very least counter intuitive, since reason dictates that when faced with the outbreak of some epidemic the best alternative is to act rather than sit idly by. But as this result shows, doing the right thing at the wrong time can lead to dire consequences.

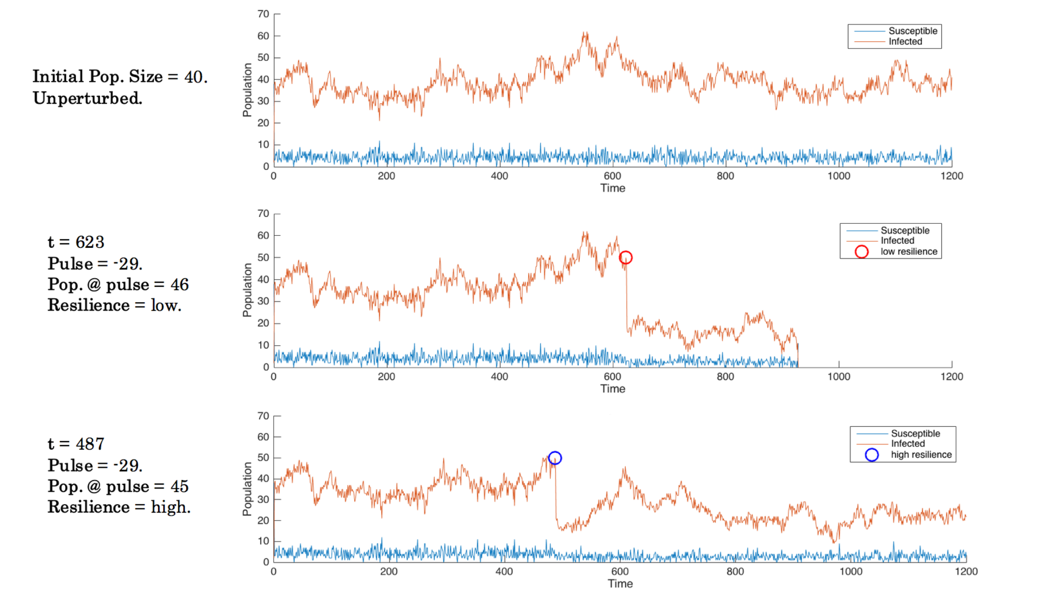

Figure 5: Results for the SIS model. **Top:** undisturbed realization of the model. After 10^7 iterations, the epidemic continues tracking the endemic state (red). **Middle:** infected population pulsed at the low-resilience state. Extinction follows shortly after. **Bottom:** infected population pulsed the the high-resilience state. System is able to resist the control, recover, and continue tracking the endemic state.

Mean Extinction Time: SIS

In addition to the individual runs presented above, the same scheme was performed for one thousand runs of the model utilizing the thresholds outlined in section 7. By comparing the mean extinction time (MTE) of the SIS runs with and without control measures, we can arrive at a quantitative measure of the effectiveness of the use of EWS analysis.

For the purpose of our simulation, we opted to vaccinate/quarantine 40 percent of the infected population once the thresholds were met. While several removal factors were implemented (30% up to 70%), we note that in our simulations, forty percent provided us with the best results, as a lower fraction proves ineffective in driving the critical transition, while higher percentages produce erratic results that do little to provide us with a clear understanding of the underlying dynamics. In essence, if the pulse is too small the effect cannot contribute to the governing dynamic in overriding the current state, while if the pulse is too big, the contribution overpowers

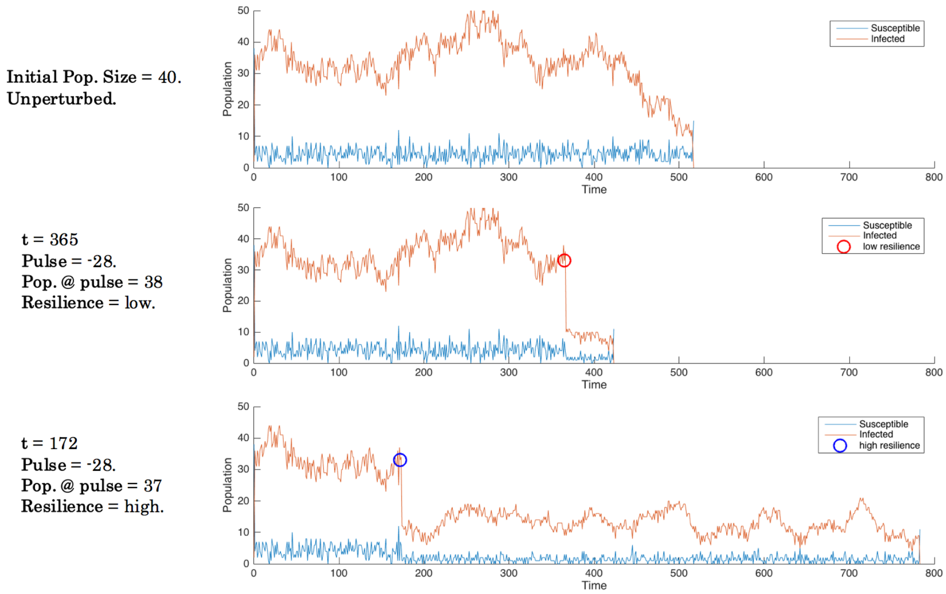

Figure 6: Results for the SIS model. **Top:** undisturbed realization of the model. System undergoes extinction on its own. **Middle:** infected population pulsed at the low-resilience state. Extinction follows shortly after. **Bottom:** infected population pulsed the the high-resilience state. As in the previous case, system is able to resist the control and recover, however, it eventually reaches extinction at a much later time than if left to its own devices. Please refer to figure 3 for metric-based analysis.

the governing dynamic without yielding any useful information.

We would also like to note that we choose not to track the quarantined/immunized population post-pulse. This decision arises from our interest in analyzing the dynamics of the remaining population, rather than the exact method by which they were extracted. Hence, in the context of this analysis it is not paramount that we carefully define how the control mechanism achieves it task, it is only important that we note that once the population in question is subjected to said controls, they are no longer allowed to interact with the remaining population. As far as the resulting dynamics is concerned, they are inconsequential.

After applying the controls to the indicated fraction of the population, we compared the results of pulsing the population at the high threshold vs. the low threshold, and finally the results without any control implementations. From one thousand runs performed using this scheme, we were able to meet the high threshold 593 times, achieving early extinction 151 times, for an MTE of 1197.2 years.

On the other hand, the low threshold was met 569 times, reaching extinction only 84 times for an MTE of 1267.4. The results confirm our hypothesis showing that pulsing the population at the high threshold is at least 10.7 percent more effective than the low threshold, resulting in a difference of 70.2 years in terms of MTE.

The numbers are far more dramatic when comparing the results of the high threshold control vs. no controls measures. Results are outlined in table 2.

The takeaway message from our results for the SIS model is that it is in our best interest to extract information from the system before we attempt to introduce controls, as we could ultimately be extending the same conditions we're trying to eliminate. Furthermore, extensive simulations show that there is an advantage in introducing controls at the high vs. low threshold when trying to induce early extinctions. Last, the difference in MTEs of the control vs. no control cases show us that EWS analysis can be an effective tool in the fight against epidemics.

Population Model with Allee Effect

For the model outlined in section 4, we conduct our trials in similar fashion to the SIS model. The parameters employed in the simulation are as follows [15]: $\mu = 0.2, \sigma = 3.0, \lambda = 1.425$. The initial population number N was set at 120, with carrying capacity $K = 100$.

As in the SIS model, we keep the population removal factor of 0.4. However, unlike the SIS model, there is no ambiguity as to the fate of the removed population, as they are exterminated post harvest, thus there is no real need to track them.

Reassuringly, the results obtained for the model with Allee effect are consistent with those of the SIS model. As hypothesized, the removal of portion of the pest population at the low-resilience state causes its collapse, while similar measures at the high-resilience state not only fail to drive an early extinction event, but as figure 7 illustrates, make conditions worse by extending the time to extinction of the pest.

Once again, this result highlights the perils of indiscriminately introducing controls without sufficient information regarding the state of the system.

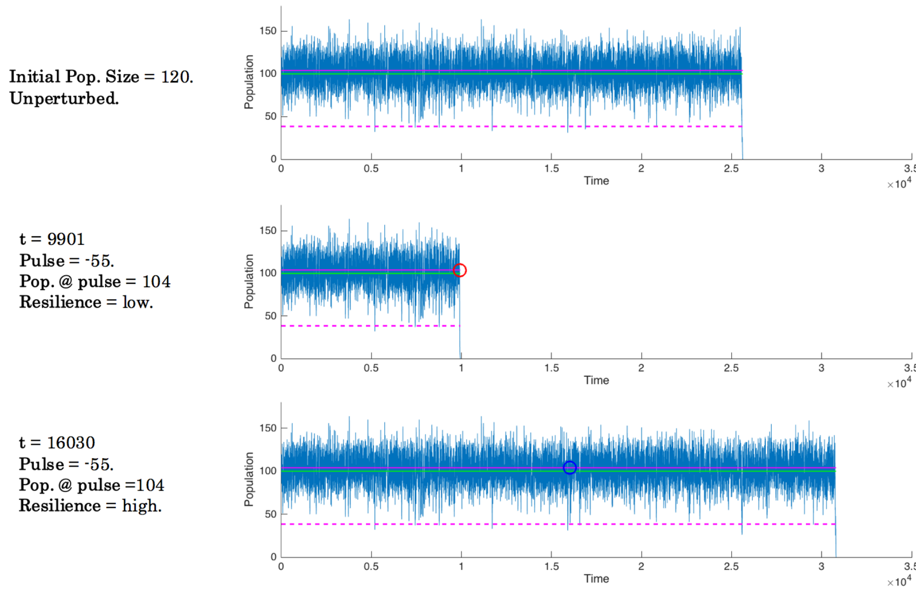

Figure 7: Results for the model with Allee effect. **Top:** undisturbed realization of the model. System undergoes extinction on its own. **Middle:** pest population pulsed at the low-resilience state. Extinction follows shortly after. **Bottom:** population pulsed the the high-resilience state. Similar to the SIS model, system is able to resist the control and recover, eventually reaching extinction at a much later time than if left undisturbed. As in the SIS model, all controls were introduced at population sizes of equal magnitude, and the quantities removed were exactly the same.

Mean Extinction Time: Allee model

One thousand runs of the Allee model with a population removal factor of 0.4 at the threshold values outlined in section 7 yielded an MTE of 7012.9 years for the high auto-correlation values, versus an MTE of 7379.3 years for the low auto-correlation value. The difference in MTEs of 366.2 years further support our hypothesis.

Table 2: mean extinction times for 1,000 runs (years)

Threshold type	SIS	Allee
high	1,197.2	7,012.9
low	1,267.4	7,379.3
no control	1,819,997.8	7,535.83

Our results show that metric-based EWS analysis is able to capture critical changes in the system state across fundamentally different models, calling to our attention the effectiveness of Early-Warning Signals theory to monitor the resilience of dynamic systems across a variety of scenarios. In addition, the control methods explored, aided by the theory, provide us with the ability to explore novel ways to solve problems of great import, where the focus is to move away from prediction towards the control of outcomes. As we've seen, the results obtained can be of great value and hopefully they will serve as the launching platform for further research in this area.

9. Further Work

Moving forward, we seek to extend our work to include the study of additional dynamical models, thus gaining a deeper understanding of the theory of Early-Warning Signals and its applicability to real world problems. Also, further scaling of the models presented here to include bigger populations, as well as large scale automated testing would enhance the robustness of the results achieved thus far, as unfortunately, the computationally expensive nature of our simulations make it a prohibitive task. Last, a more comprehensive method for determining metric indicator thresholds would provide us with more definitive results once data and simulation methods for handling bigger runs in larger populations become available.

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