Early Warning Signals for Invasive Species Populations

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# Methods

Early warning signals (EWSs) are statistical indicators of impending changes in the qualitative output of a system. These indicators appear upon the approach to a system’s bifurcation event. As the bifurcation event nears, the system’s speed of response to perturbation decreases[1]. Subsequently, the statistical behavior of the system responds to this change. By comparing the statistical behavior of datasets in which an invasive species has a significant increase in population size and does not, we determine EWSs that are artifacts of the approach to a bifurcation event.

To generate invasive species population data for analysis, we used the classic two-species Lotka-Volterra competition model[2] with the addition of an immigration term , the rate of immigration events per unit time for species to our system. represents colonizing invasive individuals that are input to the system via transplantation and serves as the perturbation that our system may have a changing response on approach to a bifurcation event.

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| **Variable** | **Meaning** | **Unit** |
|  | Abundance | Individuals |
|  | Per capita birth rate | Individuals per unit time per individual |
|  | Carrying capacity | Individuals |
|  | Interspecific competition ratio | None |
|  | Immigration rate | Individuals per unit time |

The equations above describe our two species system where species is endemic and species is invasive. The Lotka-Volterra competition model was chosen for its depth of previous study[3] and control parameters and . For reduction of covariates in the analysis of system behavior, all values other than each species interspecific competition factor and immigration rates are taken to be equal. The endemic species immigration rate is equal to zero, and the invasive species immigration rate is greater than zero.

To introduce stochasticity, each term of both equation is assumed to behave according to a Poisson probability distribution with equal to the deterministic value of a given term. The system is then simulated via a -leap algorithm[4].



Figure . Three qualitative outcomes of the model for interspecific competition factor ratios less than, equal to, and greater than one, respectively.

Now, with a model that describes invasive species population dynamics when competing with an endemic species, we must introduce a bifurcation event to the system so that its statistical behavior may change in approach. This realization type of the model is then compared to type without an approach to a bifurcation event and no persistence of immigrant invasive individuals.

To create a bifurcation event, while keeping all other parameters (other than immigration) between the species equal, we increase the ratio linearly. Thus, our bifurcation event occurs when the ratio of interspecific competition factors is equal to 1, as this is the moment the qualitative output of the model changes and the invasive species is guaranteed to competitively exclude the endemic species in the deterministic version of the model. We define the time to bifurcation, , as the time at which the model undergoes a bifurcation event. The ratio of interspecific competition factors behaves according to the linear function below.

Now, two types of model realizations can be computed: one with the bifurcation event described and eventual competitive exclusion of the endemic species by the invasive species and one with a constant, low ratio of interspecific competition factors such that immigrating individuals never establish a persistent population of invaders.



Figure . 50 realizations of the model with constant and increasing ratios of interspecific competition factors.

In determining candidate EWSs from these realizations above, we select a subset of time-series data before our bifurcation event in both realization types and compute a given statistic . These statistics are compared with a set of thresholds

Given or , we predict the type of model realization and compare with the true model realization. True and false positive rates then follow for each element of and we plot a receiver-operating characteristic (ROC) curve that visualizes the effectiveness of a statistic as an EWS.

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