Modeling critical transitions in natural systems: Can extinctions be predicted?

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Introduction

Predicting extinction is a primary concern of conservation biology. Central to guarding against species extinction in dynamically driven habitats is detecting critical thresholds in populations that result in extinction. Dynamical systems theory shows that thresholds correspond to bifurcations in population dynamics, and that a transcritical bifurcation corresponds to a population crossing a threshold from a population with a positive equilibrium size to a population that is committed to extinction. Detecting a transcritical bifurcation in a population has been limited to laboratory experiments (Drake & Griffen 2010), even though many species currently show long term declines and local extinctions. Here we developed and tested novel methods to detect a transcritical bifurcation in a population showing long term decline and eventual local extinction. We then applied these novel methods to a population of a common, but declining iconic species—the bobwhite quail.

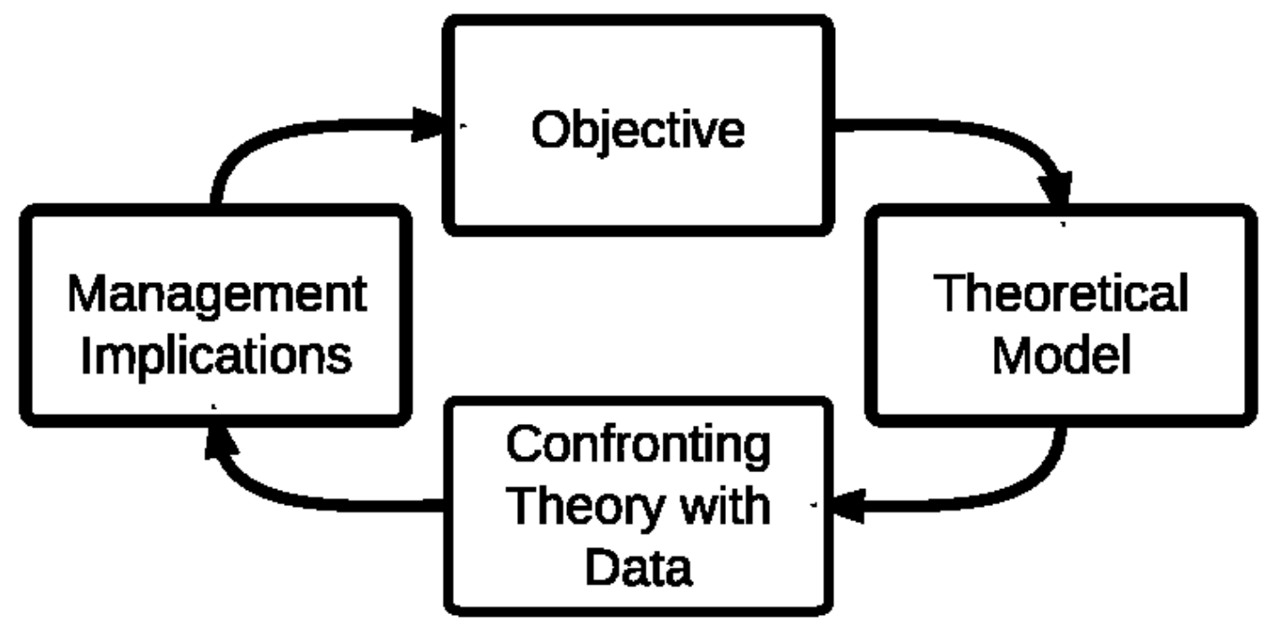

Figure 1. Flowchart of our process

Objective

Recent developments in time-series analysis has allowed researchers to fit realistic dynamical models capable of bifurcating to population data (Schooler et al. 2011). Time-series methods can detect and warn of bifurcations, but require large amounts of high quality data, complicated statistical methods, and considerable skill to transcribe dynamical system hypotheses into models. A potential alternative approach involves monitoring temporal patterns in sample statistics such as variance, skewness, and autocorrelation. For a population with a known extinction event, comparing estimated dates of bifurcations obtained from dynamical population models with those obtained from a statistical indicator would be the ultimate measure of accuracy. Finally, applying these methods to a extant managed population would illustrate and compare the utility of both methods, answering the question: can statistical indicators warn of impending bifurcations that result in extinction.

References

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Stevens, L.R., Stone, J.R., Campbell, J., & Fritz S.C. (2006) A 2200-yr record of hydrologic variability from Foy Lake, Montana, USA, inferred from diatom and geochemical data. *Quaternary Research* 65:264–274.

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Theoretical Model

We used a Bayesian multivariate state-space Gompertz dynamical population model:

$$N_{i,t+1} = N_{i,t}\, e^{a-b\ln(N_{i,t})-ct+d\ln(N_{i,t})t+\varepsilon_i}$$

$$\boldsymbol{\varepsilon} \sim MVN(\mathbf{0}, \boldsymbol{\Sigma} = \sigma_p^{\,2} I_r + \rho_p \sigma_p^{\,2} (I_r - J_r))$$

$$Y_{i,t} \sim Poisson(N_{i,t})$$

where $N_{i,t}$ is the population state of the i^{th} count at time t, a is the density independent maximum growth rate, b is the strength of density dependence, c is the time dependent constant change in a, and d is the time dependent constant change in b. For our population model it can be shown that $Var(log(N_t))/(\sigma_p^{\,2}(1-\rho_p)) \approx 1/(2b_t - b_t^{\,2})$. As process error is amplified by the nonlinearity of the Gompertz model observational error will become insignificant and $LSV_t = (1/(r-1)) \sum_1^r (log(Y_{it}) - \overline{log(Y_t)})^2$ will be an estimator of $Var(log(N_t))$. LSV is the sample variance of the log transformed population abundance estimate, which can be calculated using multiple abundance estimates at each time step or with a sliding window when only a single abundance estimate is available. The transcritical bifurcation occurs in the Gompertz model when $a_t = a - ct$ and $b_t = b - dt$ equal zero. In theory, LSV should increase to ∞ as the populations approach the bifurcation and the date that this occurs can be estimated using a generalized linear model with an inverse link function.

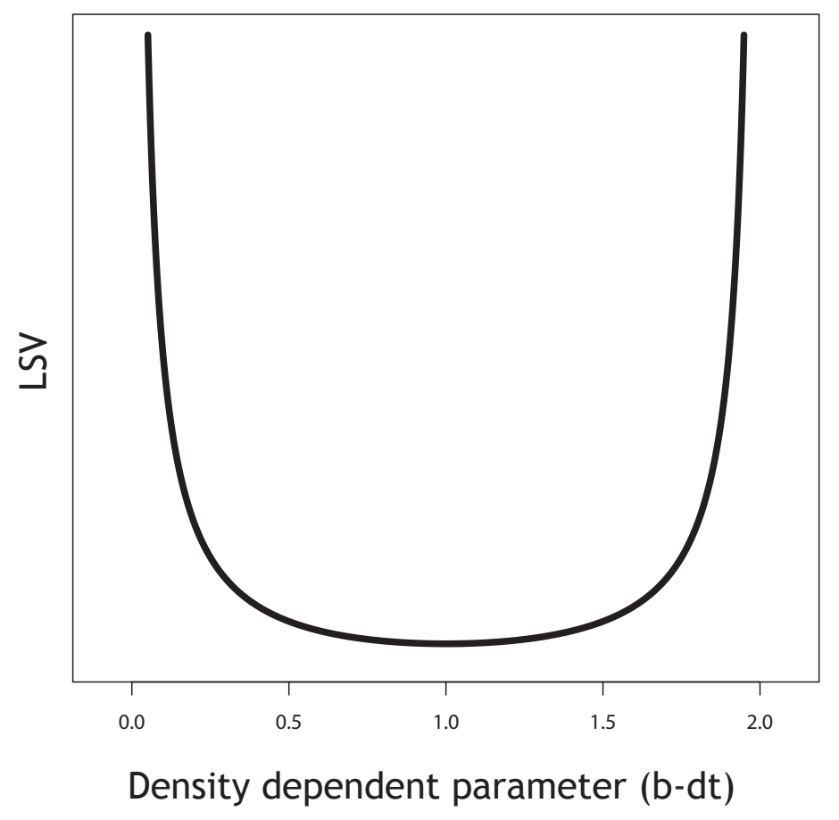


Figure 2. Theoretically expected relationship between the dynamic density dependent parameter and the indicator LSV.

Confronting Theory with Data

Samples from a continuous sediment core retrieved from the deepest basin of Foy Lake revealed that *Cymbella cymbiformis*, a common benthic diatom, experienced a local extinction at ~1500 ybp. This local extinction is timed with the dramatic transition in lake depth from low to high, brought about by increases in effective moisture (Stevens et al. 2006). This change in climate created reduced habitat for benthic species leading to a local extinction. We used percent abundance counts of diatoms from a period of decline to determine bifurcation dates. The dynamical population model showed a bifurcation at 1806 ybp (2175–1462, 95 % credible interval), and monitoring LSV alone revealed a bifurcation at 1609 ybp (1922–1188, 95% confidence interval). In this case we have >100 years warning of the extinction. Considering that this is the dominant diatom species of the shallow lake ecosystem, monitoring this species population over time increases the ability to not only predict its extinction, but also the impending regime shift of the ecosystem.

Cymbella cymbiformis

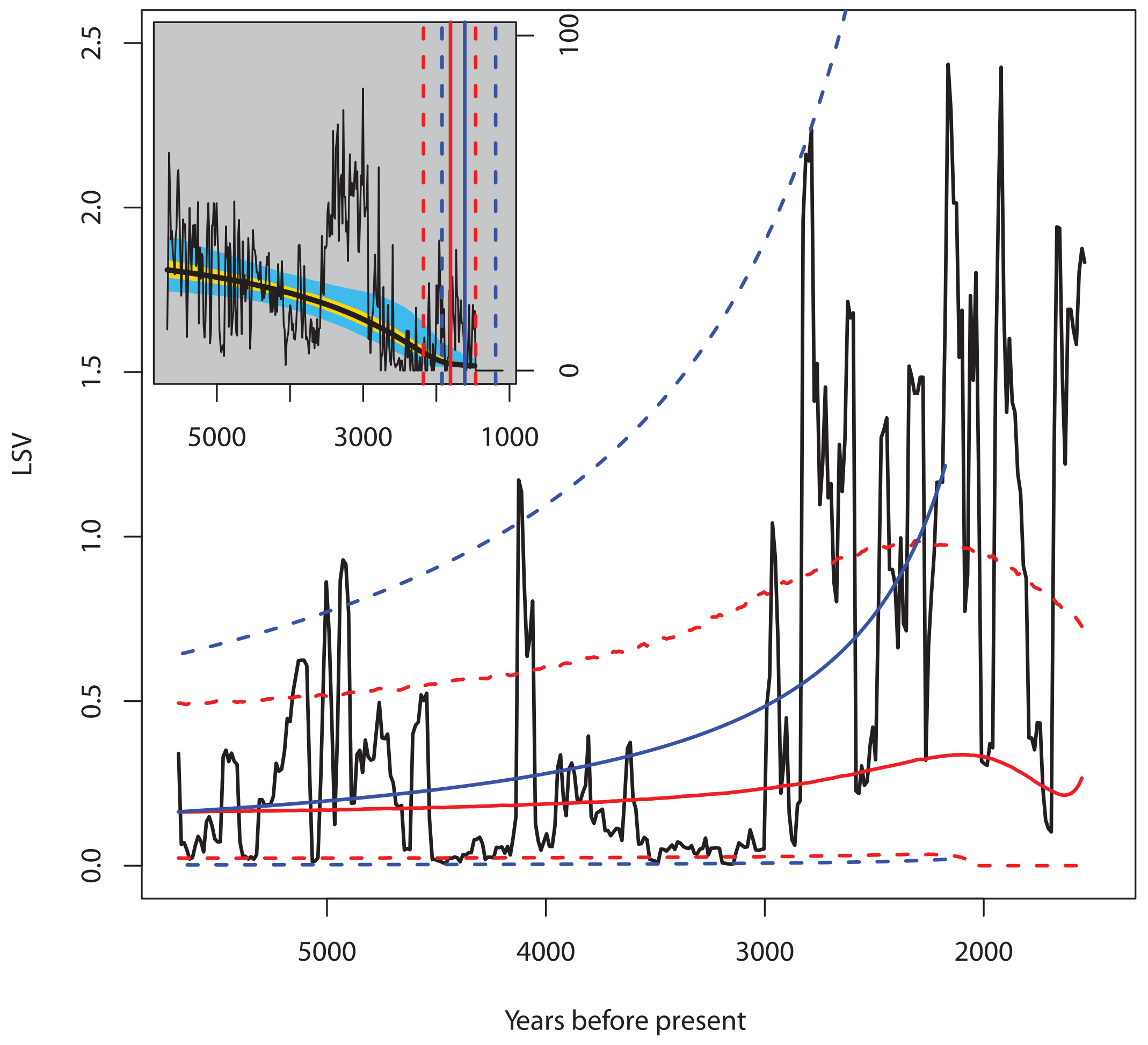
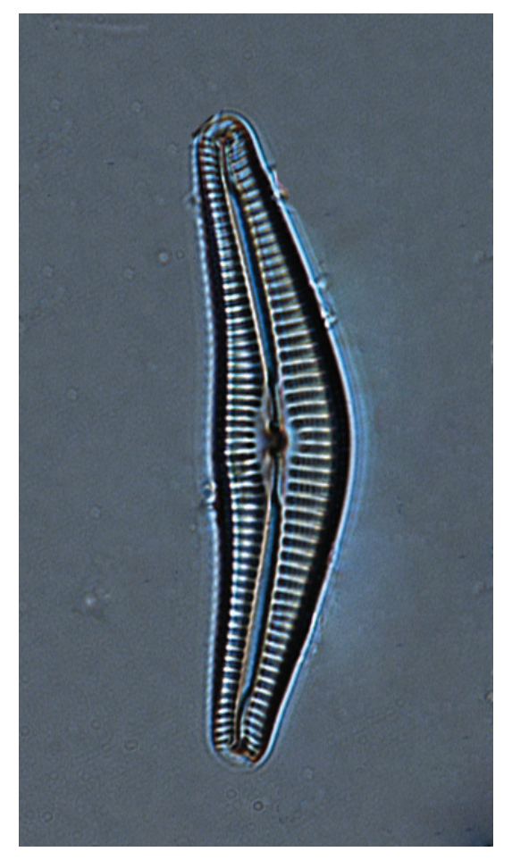


Figure 3 (left) & Figure 4 (right). Observed value of the statistical indicator LSV (black line) with the mean (red line) and 95% credible intervals (red dashes) from the posterior predictive distribution of our dynamical population model. The blue line shows the increase in LSV and 95% confidence intervals (blue dashes) obtained with partial time-series data, corresponding to the length of time covered by the blue line, and a generalized linear model. The inset plot is the observed population index (thin black line) along with the posterior median equilibrium population size (thick black line), 50% credible intervals (gold), and 95% credible intervals (blue shading). The vertical solid and dashed lines correspond to mean and 95% credible/ confidence intervals for the estimated date of the transcritical bifurcation from our dynamical population model (red) and generalized linear model (blue).

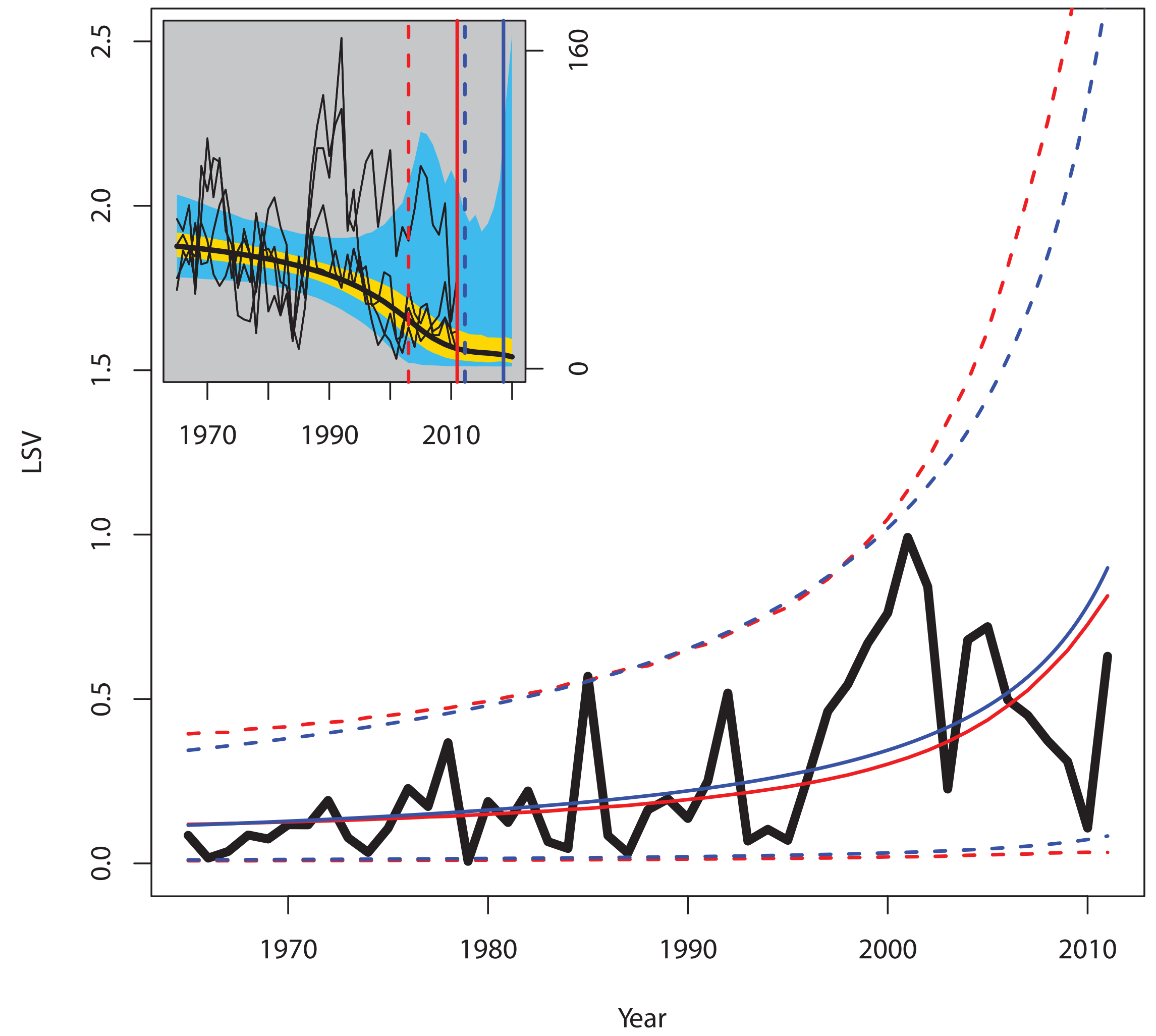


Cymbella cymbiformis

Management Implications

Northern bobwhite quail (*Colinus virginianus*) is a common bird species in agricultural regions of North America and have declined (~3.8% annually) the past 43 years over most of their range most likely due to habitat deterioration and loss. We used whistle count survey data (1965–2011) from a declining population in southeastern Nebraska, USA, where intensified agriculture has created a dynamically driven landscape. The temporal increase in LSV is similar to what is theoretically expected and to the increase observed in *Cymbella cymbiformis* which resulted in extinction. Based on our dynamical population model we predict that the transcritical bifurcation occurred in 2011 (2003–2031, 95% credible interval). Based on monitoring LSV alone, we estimate that the population will bifurcate in 2018 (2012–2029, 95% confidence interval). Regardless of when the population actually bifurcates we expect that extinction will occur soon after.

Bobwhite Quail



Conclusion - New Objectives

Our results demonstrate that thresholds that result in a commitment to extinction do exist in nature and can be detected early with minimal amounts of field data by monitoring LSV. We anticipate that the transcritical bifurcation is reversible for the northern bobwhite quail and does not result in hysteresis or immediate extinction; therefore if the driving dynamic, such as land use change, is identifiable and controllable this extinction threshold may be reversed. Furthermore, our results suggest that monitoring programs can use LSV to warn of possible thresholds in data-poor situations and monitor success of management actions to avoid possible thresholds by tracking decreases in LSV.