Ecosystem Regime Shifts: Early Warning Indicators and Non-Linear Dynamics

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A Dissertation presented to the Graduate Faculty
of the University of Virginia in Candidacy for the Degree of
Doctor of Philosophy

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University of Virginia
May, 2014

Abstract

Regime shifts are rapid, sometimes irreversible, changes to non-linear feedback mechanisms that occur when ecosystems transition between alternate stable states. Ecosystem regime shifts sometimes have severe consequences for human well being including eutrophication in lakes, desertification, and fisheries collapses. Statistical anomalies such as increased autocorrelation and variance may warn of impending shifts, indicating that adaptive management is necessary. To this effect, I proposed heteroskedasticity as a new, powerful early warning indicator for ecosystem regime shifts. Heteroskedasticity is a type of clustered variance that can occur in time series or in spatial data. I hypothesized that statistically significant heteroskedasticity would be present in ecosystems approaching regime shifts, but would not be present in ecosystems without regime shifts. I further hypothesized that tests for heteroskedasticity in time and space would minimize the occurrence of false positive warnings. I expected the null hypothesis of no significant heteroskedasticity to ease interpretation of early warning indicators and relax the need for pristine reference systems to compare to perturbed systems. I tested these hypotheses using simulated data from stochastic ecosystem models and data collected during a whole-lake regime shift experiment. The simulated data comprised regime shifts with a variety of mechanisms, but in all cases heteroskedasticity was a powerful and easily interpreted early warning indicator. In the whole-ecosystem experiment, heteroskedasticity tests warned of an impending tipping point well in advance of other indicators like autocorrelation and variance. This shows that tests for heteroskedasticity can be effective at spatial and temporal scales relevant to ecosystem management. The heteroskedasticity indicator contributed by my dissertation satisfies

practical requirements for an early warning indicator including that it is powerful, minimizes false positives, and does not require a pristine reference system. Overall, my dissertation contributes both a valuable tool for ecosystem management and for developing fundamental understanding of food webs as complex nonlinear systems.

ACKNOWLEDGEMENTS

I am extremely grateful to my supervisor, Michael Pace, for his patient guidance throughout my time as an undergraduate and graduate student. I am also grateful for the extensive guidance and the opportunities given to me by the Trophic Cascade Project PI's (Michael Pace, Stephen Carpenter, Jonathan Cole, James Kitchell, and James Hodgson) and by my dissertation committee (Paolo D'Odorico and Karen McGlathery). I would like to thank Mark Kopeny for agreeing to serve as the Dean's representative for my dissertation defense.

I would like to thank my friends, family, collaborators, and the faculty and staff of the Department of Environmental Sciences for their support while completing this research. R. Batt, C. Brosseau, T. Cline, J. Coloso, M. Dougherty, A Farrell, R. Johnson, S. Klobucar, J. Kurtzweil, K. Lee, T. Matthys, K. McDonnell, H. Pack, L. Smith, T. Walsworth, B. Weidel, G. Wilkinson, C. Yang, and L. Zinn provided critical technical help in the laboratory and field for Chapters 4 and 5.

This dissertation is based on of work funded by the National Science Foundation (DEB 0829583, Graduate Research Fellowship Program, Nordic Research Opportunity), the Virginia Space Grant Consortium (Graduate STEM Fellowship Program), the University of Virginia's Center for International Studies (Global Activities Grant Program), the Swedish Research Council (Nordic Research Opportunity), and the University of Virginia's Department of Environmental Sciences.

TABLE OF CONTENTS

CHAPTER 1: DISSERTATION INTRODUCTION

Regime shifts are rapid, sometimes irreversible, transitions between alternate ecosystem states (Scheffer et al. 2001; Scheffer and Carpenter 2003). Regime shifts may have severe consequences for human well being including eutrophication in lakes, desertification, and fisheries collapses (Scheffer et al. 2001; Scheffer and Carpenter 2003; Scheffer et al. 2009). Recent theoretical results suggest that statistical anomalies may warn of an impending regime shift, making it possible to foresee and potentially even avert catastrophic shifts by warning that adaptive management is necessary (Biggs et al. 2009; Scheffer et al. 2009; Dakos et al. 2012; Scheffer et al. 2012).

Most early warning indicators derive from the dynamical systems concept of critical slowing down (van Nes and Scheffer 2007; Scheffer et al. 2009). Critical slowing down is the progressive decline in recovery time from perturbations as a system approaches a regime shift (Scheffer et al. 2009). This slowing down manifests itself in time series as anomalous increases in autocorrelation and variance (Carpenter and Brock 2006; van Nes and Scheffer 2007; Scheffer et al. 2009). These statistics are typically calculated using moving window analyses where a window (or subset) of data from the time series of a key ecosystem property is used to calculate the early warning statistics. The statistics are then recalculated as the window is then iterated forward in time. Plots of the dynamics of early warning statistics are then evaluated for trends. Autocorrelation and variance are expected to increase prior to a regime shift, but should not both increase in stable systems (Scheffer et al. 2009; Carpenter et al. 2011). Other statistics, such as skewness, may also change in predictable ways prior to a shift (e.g. Guttal and Jayaprakash 2008).

The efficacy of early warning indicators has mainly been evaluated through analyses of data simulated from minimal models of grazing and eutrophication (e.g. Carpenter and Brock 2006; van Nes and Scheffer 2007; Scheffer et al. 2009) or through regime shift experiments in highly controlled laboratory settings (e.g. Drake and Griffen 2010; Dai et al. 2012). The efficacy of early warning indicators in field settings is unknown, in part because practical challenges such as observation error and seasonal cycles are not included in model and laboratory studies. Further, identifying trends in indicators is often subjective due to natural variability in indicators. With no benchmark values for interpretation, situations occur where the indicators respond properly prior to a shift, but managers do not interpret the dynamics as being significant. Alternatively, the indicators may vary randomly in a stable system, but managers interpret insignificant short-term trends as early warning.

This dissertation is motivated by a concern that leading indicator statistics: 1) may not be powerful enough to forecast regime shifts with sufficient time to adapt management strategies, 2) may return a large number of false positives, and 3) require substantial infrastructure in terms of a undisturbed reference system to compare to perturbed systems because early warning indicators do not have meaningful thresholds to aid interpretation (Biggs et al. 2009; Scheffer et al. 2009; Contamin and Ellison 2009; Drake and Griffen 2010; Ditlevsen and Johnsen 2010). These concerns must be resolved before leading indicators can be applied in ecosystem management. This dissertation addresses these concerns by adapting and testing statistical approaches, mainly developed in economics. The chapters, described below, are mostly the results of collaborative research as part of the Trophic Cascade Project (Carpenter et al. 2011).

Chapter 2 evaluates statistical tests for conditional heteroskedasticity as leading indicators of regime shifts. Conditional heteroskedasticity is clustered variance in time series that should be exhibited in unstable ecosystems, but not in time series from stable ecosystems. I applied moving window conditional heteroskedasticity tests to time series simulated from stochastic ecosystem models with and without regime shifts to evaluate if conditional heteroskedasticity is a powerful early warning indicator and if probability values associated with conditional heteroskedasticity tests can minimize false positive warnings and the need for reference systems. Four stochastic ecosystem models, representing different types of non-linear dynamics in continuous and discrete time with varying magnitudes of noise, were used. I found that conditional heteroskedasticity tests were powerful leading indicators of ecosystem regime shifts that minimized false positives warnings and the need for pristine reference systems. This chapter was published in *The American Naturalist* (178:442–451). Stephen R. Carpenter and Michael L. Pace contributed to this paper as co-authors.

Chapter 3 evaluates tests for heteroskedasticity as leading indicators in spatially extended data. These tests are spatial analogs to the conditional heteroskedasticity tests evaluated in the second chapter. I applied tests for spatial heteroskedasticity to simulated data from vegetation models approaching the transition from vegetated to desert state. The magnitude of spatial heteroskedasticity increased as the modeled systems approached the regime shift and heteroskedasticity was a more effective indicator than spatial autocorrelation. I conclude that tests for heteroskedasticity can contribute to the growing toolbox of early warning indicators for regime shifts in spatially explicit data. This chapter was partly inspired by a workshop "Practical Methods for Analysis of Early

Warnings for Regime Shifts" at the Santa Fe Institute. Here, I met leading researchers (including my co-author Vasilis Dakos) in early warning indicators and learned about current approaches to spatial analysis. This chapter is submitted to *Journal of Arid Environments*.

Chapter 4 is an analysis of non-linear dynamics in time series derived from a whole-ecosystem regime shift experiment. In this experiment we (the Trophic Cascade Project) slowly added predator fish to a prey fish dominated lake over the course of four years to create a regime shift in predator-prey dynamics (see Carpenter et al. 2011 for detailed overview). We measured different aspects of the food web at high frequency to assess direct evidence of the existence of alternate ecosystem states. Subsequently, I removed linear relationships from these time series using generalized autoregressive conditional heteroskedasticity models in order to test for and visualize non-linearity (e.g., Hsieh 1991). Few studies directly assess the existence of alternate ecosystem states. This is because high frequency time series are rarely collected over long enough time periods to apply nonlinearity tests or to reconstruct complex dynamics in phase spaces. Rather, most studies instead rely on indirect indicators like tests for bimodality that are unable to rule out factors other than nonlinear dynamics in causing food web shifts. Directly assessing nonlinearity: 1) confirms the existence of alternate states in a lake ecosystem, and 2) confirms that any early warning indicators are due to the experimental regime shift and not other possible causes. I found strong evidence for nonlinearity and alternate ecosystem states in the experimental data. This chapter establishes the suitability of the whole-ecosystem experiment for testing the efficacy of early warning indicators at spatial and temporal scales relevant to ecosystem management. This chapter was published in

Theoretical Ecology (6:385–394). Timothy J. Cline, Stephen R. Carpenter, and Michael L. Pace contributed to this paper as co-authors.

The fifth chapter applies moving window conditional heteroskedasticity tests to time series derived from the whole-ecosystem experiment described in the previous chapter. The tests are also applied to a stable reference system. The purpose of this chapter is to test the efficacy of conditional heteroskedasticity as an early warning indicator under field conditions, at spatial and temporal scales relevant to ecosystem managers. These scales, and difficulties associated with real data such as observation error, noise, and small sample sizes, are typically minimized when simulated data are used to test early warning theory (Carpenter 2003, Scheffer et al. 2009, Seekell et al. 2011). Using time series from the field study, conditional heteroskedasticity gave warnings up to a year and a half prior to the experimental regime shift. Early warning signals were not present in the stable reference system. We concluded that heteroskedasticity is an effective early warning indicator at spatial and temporal scales relevant to ecosystem management. This chapter was published in *Ecosystems* (15:741–747). Timothy J. Cline, Stephen R. Carpenter, and Michael L. Pace contributed to this paper as co-authors.

The sixth and final chapter briefly summarizes the main contributions of the dissertation and gives several avenues for future research. Specifically, I conclude that early warning indicators can precede regime shifts spatial and temporal scales relevant to ecosystem management. I also conclude that tests for conditional heteroskedasticity are highly effective early warning indicators because 1) they give warning far in advance of tipping points, 2) they have a built in threshold that aids in determining if a signal is meaningful, reducing the chance of false positive early warnings and eliminating the needs for a pristine reference system with which to compare signals from degrading systems. Ecosystem scale tests are necessary to further test the efficacy of early warning indicators and to test if early warning indicators appear in time for adaptive management to avert a shift. These types of tests are important potential avenues for future research.

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CHAPTER 2: CONDITIONAL HETEROSKEDASTICITY AS A LEADING INDICATOR OF ECOLOGICAL REGIME SHIFTS[1]

Abstract

Regime shifts are massive, often irreversible, rearrangements of nonlinear ecological processes that occur when systems pass critical transition points. Ecological regime shifts sometimes have severe consequences for human well-being, including eutrophication in lakes, desertification, and species extinctions. Theoretical and laboratory evidence suggests that statistical anomalies may be detectable leading indicators of regime shifts in ecological time series, making it possible to foresee and potentially avert incipient regime shifts. Conditional heteroskedasticity is persistent variance characteristic of time series with clustered volatility. Here, we analyze conditional heteroskedasticity as a potential leading indicator of regime shifts in ecological time series. We evaluate conditional heteroskedasticity by using ecological models with and without four types of critical transition. On approaching transition points, all time series contain significant conditional heteroskedasticity. This signal is detected hundreds of time steps in advance of the regime shift. Time series without regime shifts do not have significant conditional heteroskedasticity. Because probability values are easily associated with tests for conditional heteroskedasticity, detection of false positives in time series without regime shifts is minimized. This property reduces the need for a reference system to compare with the perturbed system.

Introduction

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[1] Seekell DA, Carpenter SR, Pace ML (2011) Conditional heteroskedasticity as a leading indicator of ecological regime shifts. The American Naturalist 178:442-451.

Regime shifts are reorganizations of nonlinear ecological processes that occur when systems pass critical transition points. Ecological regime shifts are sometimes irreversible and can have severe consequences for human well-being through loss of water quality, loss of rangeland or fish production, or loss of species (Carpenter and Brock 2006; Scheffer et al. 2009; Drake and Griffen 2010). Generally, the critical transition point is unknown, and regime shifts occur with little or no warning (Scheffer et al. 2009). There are a wide variety of approaches to identify regime shifts after they occur, but methods to warn of impending regime shifts are needed if unwanted transitions are to be prevented (Andersen et al. 2009; Biggs et al. 2009; Contamin and Ellison 2009).

Theoretical evidence suggests that statistical anomalies appear in ecological time series prior to regime shifts (e.g., Carpenter and Brock 2006; Carpenter et al. 2008; Scheffer et al. 2009). Increasing autocorrelation (Scheffer et al. 2009), increasing variance (Brock and Carpenter 2006; Carpenter and Brock 2006; Scheffer et al. 2009), shifts to low-frequency variance (Kleinen et al. 2003; Biggs et al. 2009), and changing skewness (Guttal and Jayaprakash 2008) in ecological time series warn of impending regime shifts in theory and are present before regime shifts in simulations of stochastic ecosystem models (e.g., Carpenter et al. 2008; Guttal and Jayaprakash 2008; Scheffer et al. 2009), as well as in laboratory studies (Drake and Griffen 2010). These indicators are thought to represent a general class of early warning signals applicable to a wide variety of regime shifts. However, some common critical transitions are characterized by decreasing variance, decreasing autocorrelation, or no change in symmetry (Berglund and Gentz 2002; Brock and Carpenter 2006; Guttal and Jayaprakash 2008; Carpenter et al. 2009). Hence, leading indicators may have ambiguous interpretations when applied to environmental data if the form of the underlying dynamics is unknown (Brock and Carpenter 2006). An additional challenge is to discern between random and nonrandom changes in indicators (Scheffer et al. 2009). Currently, a reference system is needed to compare to the perturbed system in order to interpret changes in indicators because indicators are not easily associated with probability values (e.g., Drake and Griffen 2010; Carpenter et al. 2011).

Conditional heteroskedasticity is persistence in the error variance of autoregressive time series models (Engle 1982). In time series, conditional heteroskedasticity appears as clustered volatility, such as the periods of high volatility and low volatility seen in plots of stock market returns (Engle 2001). Conditional heteroskedasticity is well known in economics, but tests for conditional heteroskedasticity and related autoregressive conditional heteroskedastic time series models have rarely if ever been applied to ecological time series (Lamoureux and Lastrapes 1990; Engle 2001). We analyzed conditional heteroskedasticity as a potential leading indicator of regime shifts in ecological time series. We use simulated time series from stochastic ecosystem models to evaluate the power of conditional heteroskedasticity to detect impending regime shifts and to evaluate the susceptibility of these tests to false positives. Some of these models use empirically measured large process error, which more adequately mimics nature than small-noise processes generally applied to ecosystem models.

Methods

Conditional Heteroskedasticity

Constant residual variance (homoscedasticity) is a fundamental assumption of ordinary least squares regression analysis. Methods for dealing with violation of the constant variance assumption (heteroskedasticity) are well studied and include weighted least squares regression, data transformations, and heteroskedastic consistent covariance estimators (e.g., Box and Cox 1964; White 1980). Similarly, stationary residual variance is also an assumption of many time series analysis methods, and many time series are heteroskedastic, with periods of high and low volatility (Engle 1982, 2001; Lamoureux and Lastrapes 1990). These time series are described as conditionally heteroskedastic, meaning that the variance at a time step is dependent or conditional on the variance at the time step before. High volatility is likely to follow high volatility, and low volatility is likely to follow low volatility, leading to a characteristic clustering of variances.

Variance increases in the vicinity of an impending regime shift due to flickering or squealing (Taylor et al. 1993; Carpenter and Brock 2006; Scheffer 2009; Brock and Carpenter 2010). Flickering occurs when stochastic forcing moves a system between two states but not permanently from one state to another (Scheffer 2009; Brock and Carpenter 2010). These back and forth changes in state variables create increased variance that can be viewed as an early warning because environmental conditions have not changed enough to force the system into one state (Scheffer 2009). Squealing occurs when variance builds in vicinity of a regime shift because the system does not recover from random environmental perturbations rapidly due to reduced return rate to equilibrium (Scheffer 2009; Scheffer et al. 2009; Brock and Carpenter 2010). Because of flickering and squealing, the region of time series near a critical transition might be a cluster of high volatility, and the region of time series more distant from the critical transition point might be a cluster of low volatility. Thus, significant conditional heteroskedasticity is expected to appear as a system approaches a critical transition point because high volatility will appear to cluster. If an impending regime shift is characterized by declining variance prior to the critical transition point, conditional heteroskedasticity will still appear because there is still a clustering of, in this case, low variance prior to the shift. There should be no significant conditional heteroskedasticity in time series without a critical transition. Figure 1 is an example of conditional heteroskedasticity. The figure consists of squared residuals from an autoregressive lag-1 time series model applied to 200 time steps of simulated planktivore biomass prior to a regime shift in a temperate-lake food web model plotted by the squared residual at the previous time step. The strong positive relationship between squared residuals and the squared residuals at the previous time step is characteristic of conditional heteroskedasticity. The regression line would be horizontal if there were no conditional heteroskedasticity and variance at one time step was not dependent on variance at the previous time step.

Analytical Approach

We used simulated time series with and without regime shifts to evaluate conditional heteroskedasticity as a leading indicator. Simulated data are well suited to evaluation of leading indicators because the locations of regime shifts due to changes in the control parameter are known exactly. The power of conditional heteroskedasticity as a leading indicator can be assessed at different distances preceding the simulated regime shift, and the indicator can be applied to simulated time series without regime shifts to evaluate its susceptibility to returning false positives. We selected four models from the literature to generate time series (Table 1) representing discrete- and continuous-time approaches with various magnitudes of noise. The models are formed from systems of stochastic difference equations or stochastic differential equations and are calibrated to either long-term observations or experimental results. The stochastic difference equations include empirically measured large process errors. The stochastic differential equations contain small-noise perturbations typical of leading indicator simulation studies (e.g., Carpenter et al. 2008). These noise terms represent environmental stochasticity but not independent random observation error due to measurement error (Carpenter 2003). The stochastic differential equations were integrated numerically using the Euler-Maruyama method for Ito calculus. The models were run in R (http://www.r-project.org) and Maple 13 (http://www.maplesoft.com).

Models

The models used in this study have been described in detail elsewhere and are described only briefly here (Table 1). The first model is a stochastic Ricker population dynamics model (May 1976; Ponciano et al. 2005) that is widely used to describe discrete-time, density-dependent population dynamics (e.g., Beard et al. 2003; Ponciano et al. 2005). Model parameters, including process error, were derived from laboratory cultures of *Escherichia coli*, using maximum likelihood methods by Ponciano et al. (2005). When the model growth rate (see Table 1) is raised past the critical transition point, the system undergoes a period doubling (pitchfork) bifurcation. We simulated 2,000 time steps at a stable point as a reference series with no regime shift. We then simulated 2,000 time steps with slowly increasing population growth rate so that the system would pass the critical transition point at time step 1,500.

The second model describes the discrete-time dynamics of a midge-algae-detritus food web in Lake Myvatn, Iceland (Ives et al. 2008). The model parameters, including process error, were derived from long-term data, using maximum likelihood methods by Ives et al. (2008). We generated a reference series of midge biomass with no regime shift by setting the algal growth rate low so that midge dynamics remained at a stable point. We simulated a 2,000-step time series of midge biomass with regime shift by slowly increasing the algal growth rate to mimic eutrophication, with the result that the critical transition point is crossed at step 1,500. We applied conditional heteroskedasticity tests to the resulting midge time series. To find the transition point, we simulated the deterministic skeleton of the model and labeled the point just before oscillations begin as the critical transition point. After the critical transition point is crossed, this equation undergoes a supercritical Neimark-Sacker bifurcation (a discrete-time Hopf bifurcation), which is characteristic of a system that loses fixed-point stability and moves toward periodic or quasi-periodic behavior (Ives et al. 2008).

The third model is a simple continuous logistic growth equation that describes *Daphnia magna* population dynamics in a laboratory experiment (Drake and Griffen 2010). Drake and Griffen (2010) progressively decreased food supply to populations of *Daphnia* over the course of several weeks, leading to declines in abundance and eventually extinction. Declines in both population growth rate and system carrying capacity are expected when food supply is diminished (Griffen and Drake 2008; Drake and Griffen 2010). We generated a reference series of *Daphnia* biomass by simulating 2,000 time steps at a stable equilibrium. We generated a series with regime shift by simulating 2,000 time steps with slowly decreasing intrinsic growth rate and decreasing carrying capacity so that the system crosses the critical transition point at time step 1,500 and undergoes a transcritical bifurcation. We did not allow the population to become extinct so that we could continue to apply conditional heteroskedasticity tests to the end of the 2,000-step time series. Small noise was added because process error was not estimated empirically by Drake and Griffen (2010).

The fourth model describes planktivore-zooplankton-phytoplankton food web dynamics in a temperate lake. The model parameters were derived from long-term data by Carpenter et al. (2008). Small noise was added because process error was not estimated empirically (Carpenter et al. 2008). We generated a reference series of planktivore biomass by simulating 2,000 time steps at a stable equilibrium with high predation pressure on planktivores. This system has low planktivore biomass, high zooplankton biomass, and low phytoplankton biomass. We generated a series with regime shift by slowly reducing predation pressure on the planktivores to simulate overfishing of predatory fish. The system crosses the critical transition point for a fold bifurcation at time step 1,500, and there is a trophic cascade characterized by increasing planktivore biomass, declining herbivore biomass, and increasing phytoplankton biomass. The planktivore biomass time series is used in this analysis of conditional heteroskedasticity. The herbivore biomass time series and phytoplankton biomass time series are considered in further analysis described below.

Test for Conditional Heteroskedasticity

We tested for conditional heteroskedasticity in the model time series with a simple and widely used Lagrange multiplier test described by Engle (1982; see also Engle et al. 1985). The testing procedure is as follows:

(1) fit a lag-1 autoregressive model by using ordinary least squares regression,
(2) square the residuals obtained from step 1,
(3) lag the squared residuals from step 2 by one time step,
(4) regress the squared residuals from step 2 by the lagged squared residuals from step 3,
(5) calculate the Lagrange multiplier test statistic as the product of the r^2 value from the auxiliary regression in step 4 and sample size from the auxiliary regression in step 4, and
(6) calculate the probability value for the Lagrange multiplier by comparing the Lagrange multiplier test statistic to a x^2 distribution with 1 df.

Worked examples of the test calculations with and without conditional heteroskedasticity are provided in Appendix 1 in this dissertation. Generally, leading indicators are applied using moving-window analysis (e.g. Scheffer et al. 2009). Here we apply the Lagrange multiplier test for conditional heteroskedasticity to 200 time step windows. At time *t*, the value for *t* and the 199 previous time steps are included in the window. We move the window forward 50 time steps in between each test. In our model analyses, the time series have 2,000 observations so that 37 tests are applied with each test, consisting of 200 observations. We applied these tests in Minitab 15 (http://www.minitab.com).

A likely outcome is recording some significant tests even if there is no conditional heteroskedasticity and no impending regime shift. If the critical level of significance for conditional heteroskedasticity tests is 0.05, five significant tests are expected per 100 tests conducted when there is no conditional heteroskedasticity. A Bernoulli expansion may be used in conjunction with the moving-window test results in order to find the probability of returning a given number of significant tests in the total number of tests (Wilkinson 1951; Moran 2003). For example, if there is one significant test in 10 tries, we might not, without other evidence, conclude that there is an impending regime shift because the probability of finding one significant test in 10 is high ($P = 0.315$). The probability by Bernoulli expansion is calculated as

$$p = \left[\frac{N!}{(N-K)!K!} \times a^K (1-a)^{N-K}\right],$$

where N is the number of tests conducted, K is the number of significant tests, and a is the level of significance (e.g., $a = 0.05$) for the individual conditional heteroskedasticity tests (Moran 2003). Lookup tables for probability values from this equation are available in Wilkinson (1951).

Variable Selection

Leading indicators of regime shifts might be effectively resolved in time series data collected by standardized environmental monitoring programs (Brock and Carpenter 2006). However, environmental monitoring programs cannot record all variables of interest, and it may be difficult to choose variables that may be important for warning of a future regime shift (Lovett et al. 2007). We applied the moving-window Lagrange multiplier test for conditional heteroskedasticity (window width, 200) to the simulated phytoplankton and zooplankton biomass time series from the temperate-lake food web model to evaluate how variable selection from environmental monitoring may affect conditional heteroskedasticity as a leading indicator.

Results

Conditional Heteroskedasticity as a Leading Indicator of Regime Shifts

The discrete-time *Escherichia coli* dynamics model shifts toward chaotic behavior as the growth rate increases past the critical transition point and the data pitchfork, a pattern characteristic of the period-doubling bifurcation (Fig. 2A, black dots). The reference series was variable around a stable point and had no long-run change in *E. coli* abundance (Fig. 2A, red line). There was significant conditional heteroskedasticity prior to the critical transition in the time series with a regime shift, and significant tests appeared consistently before the transition point (Fig. 2B, black line). The cumulative number of significant tests was significant, as judged by Bernoulli expansion ($P < 0.05$) at time step 450. In the reference time series, there was one significant conditional heteroskedasticity test in 37 applications (Fig. 2B, red line). This frequency of occurrence is not significant as judged by Bernoulli expansion.

The midge biomass dynamics from the discrete-time food web model for Lake Myvatn transition from a stable point to oscillating behavior as algal growth rate is slowly increased (Fig. 2C, black line). Midge biomass began oscillating prior to algal growth rate being pushed across the critical transition point, indicating that environmental stochasticity plays an important role in determining the state of the system. Flickering between the stable point and oscillating regimes appears to occur between time steps 500 and 1,000. The reference system had considerable variability but remained about the stable point throughout the time series (Fig. 2C, red line). Significant tests accumulated for the transition case, and the frequency of significant tests was significant by time step 700 (Fig. 2D, black line). The significant tests occurred mainly while the system was flickering, and there were few or no significant conditional heteroskedasticity tests when the time series was at the stable or oscillating regime. This result underscores the potential importance of flickering in facilitating detection of early warnings of impending regime shifts. There was one significant test in 37 applications to the reference time series (Fig. 2D, red line). This frequency of occurrence is not significant as judged by Bernoulli expansion.

The time series from the continuous *Daphnia* dynamics model with critical transition (Fig. 3A, black line) had steady population decline, while the *Daphnia* dynamics time series without critical transition varied around a stable point (Fig. 3A, red line). There was a steady increase in cumulative number of significant conditional heteroskedasticity tests prior to the transition in the series with regime shift. The cumulative number of significant tests was significant, as judged by Bernoulli expansion, by time step 450 (Fig. 3B, black line). In the reference time series, there were two significant tests in 37 applications (Fig. 3C). This number of significant tests is not significant as judged by Bernoulli expansion.

The planktivore biomass time series with critical transition from the continuous lake food web model demonstrated logistic growth and had significant conditional heteroskedasticity throughout the period approaching the regime shift, and the impending regime shift was identified by time step 450 (Fig. 3C, 3D, black lines). The reference series varied steadily near an equilibrium value in the reference time series (Fig. 3C, red line). There were no significant conditional heteroskedasticity tests in the 37 tests applied to the reference time series (Fig. 3D, red line).

Variable Selection

Variable selection for detecting the regime shift was important in the continuous temperate-lake food web model. While there is clear early warning in the planktivore biomass series (Fig. 3C), there is no clear early warning in the zooplankton biomass time series (Fig. 4A). Herbivore biomass decreased as planktivore biomass increased (Fig. 4A, black line), but there was no consistent significant conditional heteroskedasticity (Fig. 4A, red line). Phytoplankton biomass increased as zooplankton biomass decreased (Fig. 4B, black line). There was significant conditional heteroskedasticity prior to the critical transition point (in the planktivore time series), but this was not consistent through the time series (Fig. 4B, red line). The phytoplankton time series provides early warning as quickly as the planktivore biomass series as judged by Bernoulli expansion; however, the number of significant tests is less compelling than the planktivore series when plotted (Fig. 4B). The discrepancy in consistency in returning significant conditional heteroskedasticity tests demonstrates the importance of selecting relevant environmental parameters for long-term monitoring and application of conditional heteroskedasticity as a leading indicator of regime shifts. Finding appropriate parameters to measure for real systems will be a subjective task based on modeling studies and researchers' expert knowledge of the systems they are studying (e.g., Carpenter et al. 2011).

Discussion

Conditional heteroskedasticity is a powerful leading indicator of impending regime shifts. Cumulative tests for conditional heteroskedasticity warn of regime shifts hundreds of time steps ahead of critical transition points. Conditional heteroskedasticity is robust and is effective for forecasting a variety of forms of regime shift. This is because both increasing and decreasing variance prior to a shift appear as clustered volatility prior to the shift.

Some indicators are ambiguous when the underlying dynamics of the system are unknown (Brock and Carpenter 2006). For instance, variance in water column phosphorus increases prior to the critical transition from an oligotrophic state to a eutrophic state in lake ecosystem models (Carpenter and Brock 2006). However, variance in algal biomass declines in models describing the transition of phytoplankton communities to dominance by toxic cyanobacteria during eutrophication (Carpenter et al. 2009). Hence some understanding of the potential regime shift is necessary to judge the practical importance of increases and decreases in variance. Here, we have shown that a test for conditional heteroskedasticity is effective for warning of a variety of critical transitions and could be applied to systems with increasing or decreasing variance prior to a regime shift. Association with probability values eases interpretation of test results.

Tests for conditional heteroskedasticity require much larger samples than descriptive statistics such as variance and autocorrelation (see Engle et al. 1985). This is unlikely to be problematic for parameters that are easily measured *in situ* at high frequency, such as chlorophyll-a in lakes (Carpenter et al. 2009). However, this sample size requirement could be problematic for properties that cannot be sampled at high resolution, such as fish biomass and many other ecological variables. Hence, conditional heteroskedasticity tests will be practical for application only to some variables and studies with high numbers of observations.

Increased attention will be needed to minimize false positives as the effectiveness of leading indicators is tested in theory and in field applications. False positives are cases where statistics falsely indicate an impending regime shift. False positives could lead to expensive, inconvenient, and unnecessary changes in population or ecosystem management. It is difficult to demonstrate the successfulness of avoiding regime shifts because success is essentially equivalent to no state change (Scheffer 2009). If this difficulty is combined with an abundance of false positives, policy makers and public confidence in the usefulness of programs designed to inhibit regime shifts could erode. Thus, while these indicators should be pursued, future evaluations of regime shift indicators should include time series without regime shifts to evaluate the potential susceptibility of indicators to returning false positives. In this study, by associating probability values with the conditional heteroskedasticity indicator, we were able to minimize false positives due to chance. However, false positives may also be triggered by confounding trends in external perturbations (Scheffer 2009). Thus, field studies are necessary to more adequately evaluate leading indicators.

In simulation, leading indicators should be evaluated against models with empirically measured process error to better mirror real-world perturbations. Such models may have interesting and unexpected dynamics. For instance, the midge biomass time series we used contains flickering and an unexpected early transition to the oscillating state due to environmental stochasticity. Such complex dynamics, not seen in the other models in this analysis, may be more adequately captured in models with more realistic large noises. Further, the response of some indicators may vary considerably, depending on the magnitude of noise in the system (Berglund and Gentz 2002). Thus, indicators should also be evaluated against models with a variety of magnitudes of noise.

Observation errors and biases may also be added to simulated data to more adequately mimic field data (Carpenter 2003). Parameters are associated with unique levels of observational error, and this may reduce the power of some indicators to identify impending regime shifts (Carpenter 2003). Magnitude of observation error may be dependent on sampling frequency, and high-frequency measurements (e.g., every 5 min) may be superior for practical application because they may record at a more ecologically relevant timescale than low-frequency measurements (e.g., weekly). Improved statistical power due to increased sampling size with high-frequency data will likely offset any decreased power to identify impending regime shifts due to observation error. In an experimentally induced ecosystem regime shift, Carpenter et al. (2011) found strong early warning signals in high-frequency data, and large data sets may be needed to uncover nonlinear dynamics in all complex systems.

Leading indicators such as conditional heteroskedasticity may fail to provide early warning of regime shifts (false negative) if the system is driven rapidly across the critical transition point or if an unlikely and large shock pushes the system from one stable equilibrium to another (Scheffer et al. 2009). The mechanics of the system may also cause leading indicators to fail, and it may be impossible in practice to know whether this is the case prior to a regime shift occurring. However, models thought to adequately represent nonlinear ecosystem dynamics are characterized by leading indicators prior to a regime shift (e.g., van Nes and Scheffer 2007; Carpenter et al. 2008; Scheffer et al. 2009). Laboratory (Drake and Griffen 2010) and whole-ecosystem (Carpenter et al. 2011) experimental regime shifts, as well as paleoclimate records (Dakos et al. 2008), are characterized by dynamics with early warnings prior to a regime shift. Given that conditional heteroskedasticity is expected prior to shifts, the probability of false negatives will be determined largely by the sample size that each test is applied to (Engle et al. 1985).

Leading indicators of regime shift have been successfully applied to reconstructed time series of climate transitions in the ancient past (Dakos et al. 2008). However, the true utility of regime shift indicators will not be established until they are adequately evaluated on transitions that occur at temporal and spatial scales that are relevant to policy makers and the public (e.g., Carpenter et al. 2011). Field studies that experimentally induce regime shifts are necessary to examine the advantages and limitations of different indicators and to resolve potential discrepancies in their practical interpretations.

Acknowledgements

This paper is based on work was supported by the National Science Foundation (DEB-0716869 and DEB-0917696) and the University of Virginia Department of Environmental Sciences. W. Brock, A. Ellison, K. Hondula, and an anonymous reviewer provided helpful comments that improved the manuscript.

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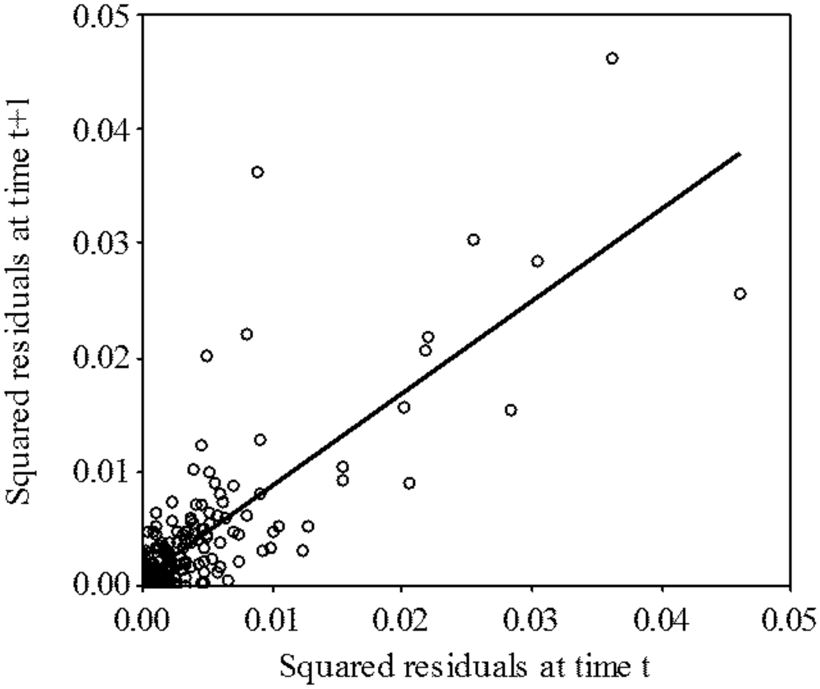

Figure 1: Squared residuals from an AR-lag 1 model applied to the two hundred time steps prior to regime shift in the planktivore biomass time series from the temperate lake food-web model plotted by the previous squared residual. The strong positive relationship is indicative of conditional heteroskedasticity because there is a relationship between the error variance at a given time step and the error variance at the previous time step. If the regression line was horizontal, error variance would have no relationship with error variance at previous time steps and there would be no conditional heteroskedasticity.

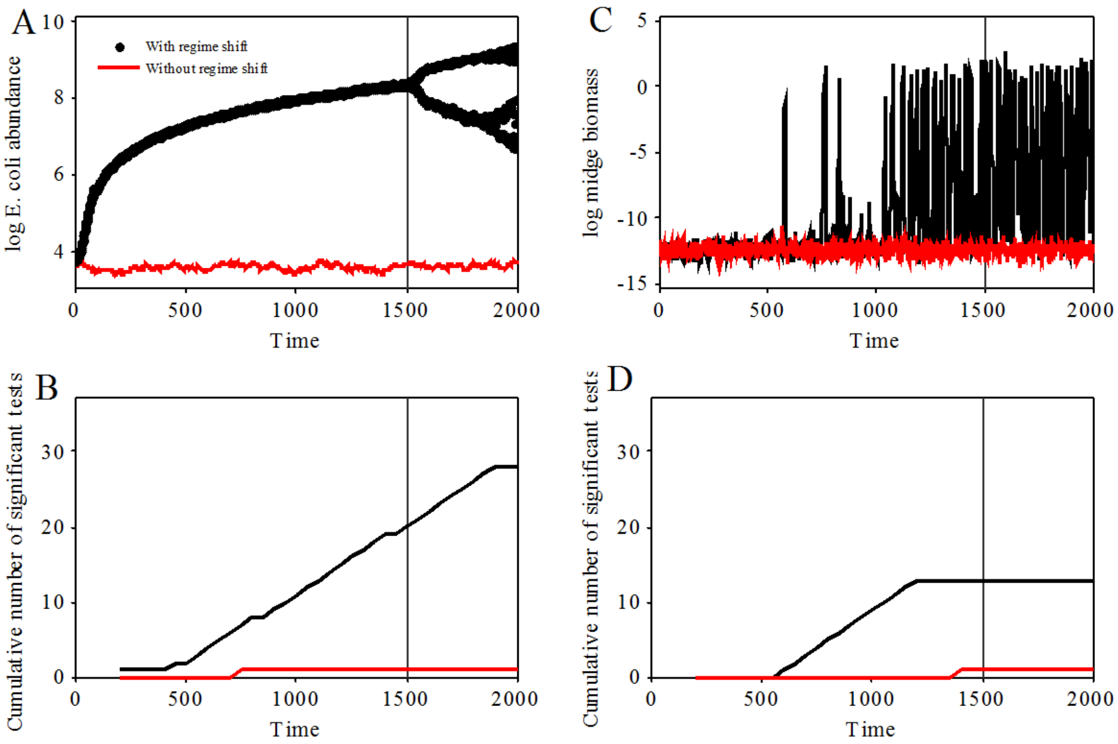

Figure 2. A) Time series from the discrete *E. coli* dynamics model with (black line) and without (red line) a regime shift. B) Cumulative number of significant moving window Lagrange Multiplier tests for conditional heteroskedasticity applied to the discrete *E. coli* dynamics model time series with (black line) and without (red line) regime shift. There are 37 total tests applied to the time series. C) Time series midge biomass from the discrete lake food-web model with (black line) and without (red line) a regime shift. D) Cumulative number of significant moving window Lagrange Multiplier tests for conditional heteroskedasticity applied to midge biomass time series from the discrete lake food-web dynamics model time series with (black line) and without (red line) regime shift. There are 37 total tests applied to the time series. The vertical gray line at step 1500 denotes the critical transition point for the control parameter in both models with regime shift.

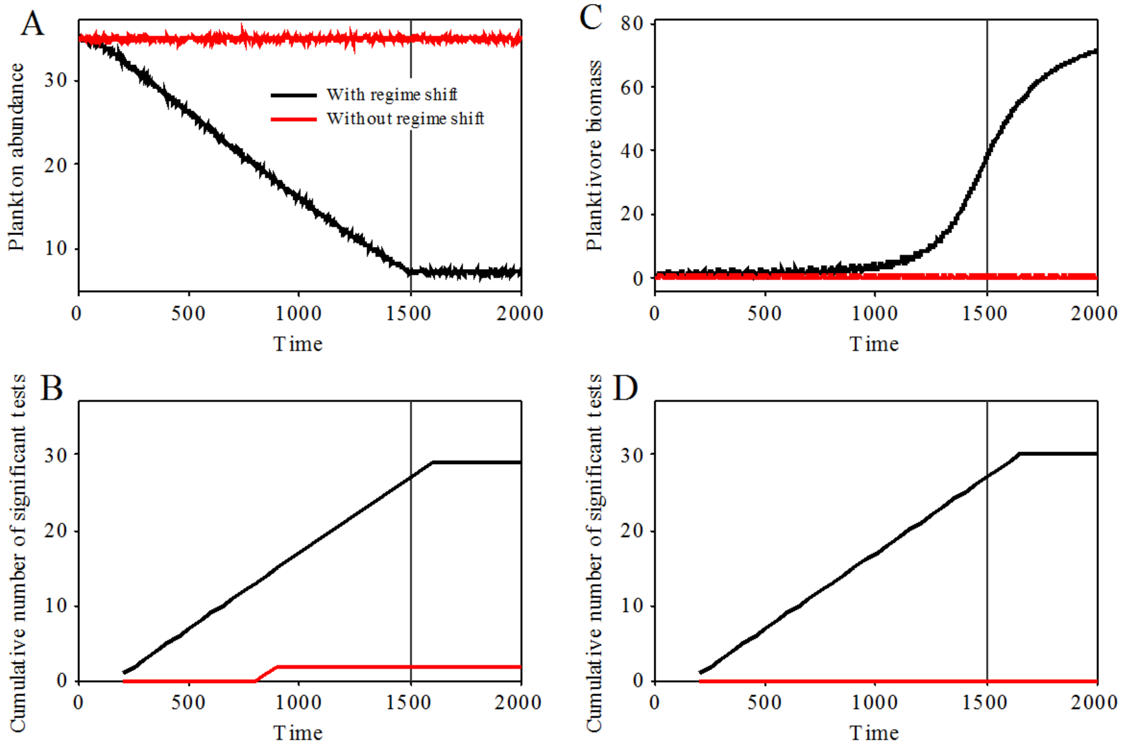

Figure 3. A) Time series from the continuous *Daphnia* dynamics model with (black line) and without (red line) a regime shift. B) Cumulative number of significant moving window Lagrange Multiplier tests for conditional heteroskedasticity applied to the continuous *Daphnia* dynamics model time series with (black line) and without (red line) regime shift. There are 37 total tests. C) Planktivore biomass time series from the continuous lake food-web model with (black line) and without (red line) a regime shift. D) Cumulative number of significant moving window Lagrange Multiplier tests for conditional heteroskedasticity applied to the continuous lake food-web dynamics model time series with (black line) and without (red line) regime shift. There are 37 total tests. The vertical gray line at step 1500 denotes the critical transition point.

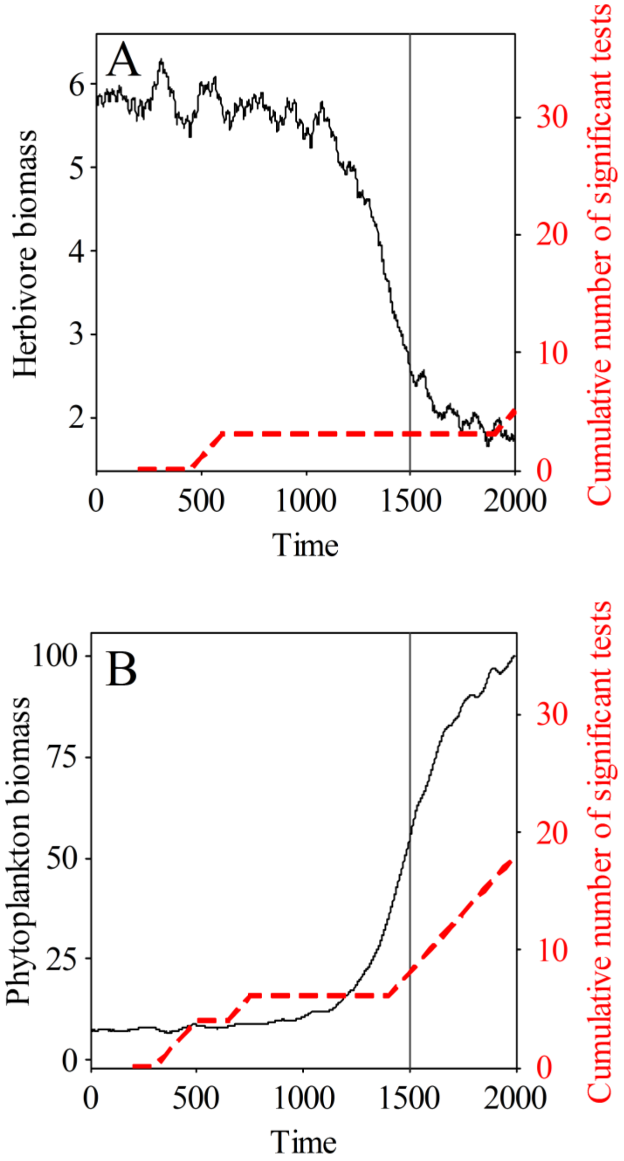

Figure 4. A) Zooplankton (herbivore) biomass from the continuous lake food-web dynamics model with regime shift (black line). B) Phytoplankton biomass from the continuous lake food-web dynamics model with regime shift (black line). The cumulative numbers of significant moving window conditional heteroskedasticity tests are the red dashed lines. The vertical grey lines denote the location of the critical transition in the planktivore dynamics. A total of 37 tests were applied to each time series.

Table 1: Ecological models and parameter values used in this study

Description	Model	Parameters
Escherichia coli growth (Ponciano et al. 2005)	$N_{t+1} = N_t \exp(a + bN_t + \sigma^2 z_t)$	N_t (population size at time t), $a = .01782$ (growth rate, control parameter), $b = -.0004802$ (density effect on growth), $\sigma^2 = .0002713$, $z_t = N(0, \sigma^2)$
Midge dynamics in Lake Myvatn, Iceland (Ives et al. 2008)	$x_{t+1} = r_1 x_t[1 + (x_t/R_t)]^{-q} \exp(\varepsilon_{1t})$, $y_{t+1} = [r_2 y_t(1 + y_t)^{-1} - (y_t/R_t)x_{t+1} + c] \exp(\varepsilon_{2t})$, $z_{t+1} = [dz_t + y_t - (pz_t/R_t)x_{t+1} + c] \exp(\varepsilon_{3t})$, $R_t = y_t + pz_t$	x_t (midge abundance at time t), $r_1 = 3.87$ (intrinsic growth rate of midges), $q = .903$ (strength of density-dependent midge dynamics), $\varepsilon_{1t} = N(0, .349)$ (random noise), y_t (abundance of algae at time t), r_2 (intrinsic growth rate of algae, control parameter), $c = 10^{-6.435}$ (input rate of algae and detritus from outside the system), $\varepsilon_{2t} = N(0, .75)$ (random noise), z_t (abundance of detritus at time t), $d = .552$ (retention rate of detritus), $p = .0666$ (quality of detritus relative to algae), $\varepsilon_{3t} = N(0, .75)$ (random noise), R_t (resource abundance at time t)
Daphnia population growth (Drake and Griffen 2010)	$dN/dt = rN[1 - (N/k)] + \sigma(dW/dt)$	N is population abundance (initial value = 35); k is carrying capacity (initial value = 35, control parameter); r is intrinsic rate of increase (initial value = 1, control parameter); $\sigma = 17.5$
Food web dynamics in a northern temperate lake (Carpenter et al. 2008)	$dA/dt = -qEA$, $dF/dt = D_F(F_R - F) - C_{FA}FA + \sigma_F(dW_F/dt)$, $dJ/dt = -C_{JA}JA - [C_{JF}vFJ/(h + v + c_{JF}F)]$, $dH/dt = D_H(H_R - H) + \alpha C_{HP}HP - C_{HF}HF + \sigma_H(dW_H/dt)$, $dP/dt = r_p L\gamma(I_0, P)P - mP - C_{PH}HP + \sigma_P(dW_P/dt)$	qE (harvest rate, control parameter), A (adult largemouth bass biomass), F (planktivore biomass), J (juvenile largemouth bass biomass), H (zooplankton biomass), $D_F = .1$ (diffusion parameter for planktivores), F_R (refuge reservoir of planktivore biomass), $C_{FA} = .3$ (consumption coefficient of planktivores by adult piscivores), $\sigma_F = \sigma_H = \sigma_P = .1$ (standard deviation of stochastic processes, same units as F, H, and P, respectively), $\alpha = .3$ (conversion of consumed phytoplankton phosphorus to zooplankton phosphorus), $C_{JA} = .001$ (consumption coefficient of juvenile piscivores by adult piscivores), $C_{JF} = .5$ (consumption coefficient of juvenile piscivores by planktivores), $v = 1$ (vulnerability parameter for juvenile piscivores), $D_H = .5$ (zooplankton diffusion parameter), $h = 8$ (refuging parameter for juvenile piscivores), $C_{PH} = .25$ (consumption rate of phytoplankton by zooplankton), $L = .6$ (phosphorus load), $\gamma(I_0, P)$ (light function based on surface irradiance $I_0 = 300\ \mu\mathrm{E\ m^{-2}\ s^{-1}}$ and phytoplankton biomass), $C_{HF} = .1$ (consumption rate of zooplankton by planktivores), P (phytoplankton biomass), $r_p = 3$ (phytoplankton growth parameter per unit phosphorus load), $m = .1$ (mortality rate of phytoplankton), $H_r = 100$ (density that plankton refuge supports)

Note: The first model is a Ricker population dynamics model (period-doubling bifurcation) of *E. coli* growth. The second model describes midge-algae-detritus dynamics in Lake Myvatn, Iceland (Neimark-Sacker bifurcation). The third model is a logistic population dynamics model (transcritical bifurcation) for *Daphnia magna*. The fourth model describes temperate-lake food web dynamics when predation pressure from apex predators is altered (fold bifurcation).

CHAPTER 3: HETEROSKEDASTICITY AS A LEADING INDICATOR OF DESERTIFICATION IN SPATIALLY EXPLICIT DATA[2]

Abstract

Regime shifts are abrupt transitions between alternate ecosystem states including desertification in arid regions due to drought or overgrazing. Regime shifts may be preceded by statistical anomalies such as increased autocorrelation and increased variance, indicating declining resilience and warning of an impending shift. Tests for conditional heteroskedasticity, a type of clustered variance, have proven powerful leading indicators for regime shifts in time series data, but an analogous indicator for spatial data has not been evaluated. A spatial analog for conditional heteroskedasticity might be especially useful in arid environments where spatial interactions are critical in structuring ecosystem pattern and process. We tested the efficacy of a test for spatial heteroskedasticity as a leading indicator of regime shifts with simulated data from spatially extended vegetation models with scale-dependent and scale-free patterning. These models simulate shifts from conditions of extensive vegetative cover to bare, desert-like conditions. We compared the efficacy of spatial heteroskedasticity as a leading indicator to the efficacy of Moran's I index of spatial autocorrelation. The magnitude of spatial heteroskedasticity increased consistently as the modeled systems approached a regime shift from vegetated to bare, un-vegetated state. Relative to spatial autocorrelation, spatial heteroskedasticity increased earlier and more consistently. We conclude that tests for spatial heteroskedasticity can contribute to the growing toolbox of

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[2] Seekell DA, Dakos V (in review) Heteroskedasticity as a leading indicator of desertification in spatially explicit data. *Submitted to Journal of Arid Environments, February 2014.*

early warning indicators for regime shifts analyzed with spatially explicit data.

Keywords: regime shift; early warning indicator; spatial pattern; heteroskedasticity; critical transition; spatial autocorrelation; resilience; desertification

Introduction

Vegetated ecosystems in arid regions are subject to desertification due to drought and overgrazing (Rietkerk et al. 2004; Kefi et al. 2007a; D'Odorico et al. 2013). Desertification is caused by changes in interactions and feedback cycles that facilitate plant growth (Peters et al. 2006; D'Odorico et al. 2013). For instance, plant cover decreases soil water evaporation and increases soil infiltration capacity, creating a feedback where plant-cover facilitates nearby plant growth (HilleRisLambers et al. 2001; D'Odorico et al. 2007). If grazing or drought reduces plant cover, a system can transition to a new cycle of decreased plant cover and increased water loss, leading to desertification (D'Odorico et al. 2007; D'Odorico et al. 2013). This type of transition between feedbacks, which may be irreversible, is known as a regime shift (Scheffer et al. 2001). In the case of desertification, a regime shift may occur by different mechanisms at different scales, all with potentially devastating losses of ecosystem services (Peters and Havstad 2006; D'Odorico et al. 2013). Because arid regions are home to more than 2 billion people including many populations with food insecurity and poor states of human well-being, there is a need to understand both the global extent of desertification and the areas most at risk of loss of resilience and transition to desert (e.g. Reynolds et al. 2007; Kefi et al. 2007a; Dakos et al. 2011; D'Odorico et al. 2013).

Statistical signatures such as increased autocorrelation and increased variance in key ecosystem properties may be leading indicators of regime shifts (Scheffer et al. 2009; Carpenter et al. 2011; Dakos et al. 2012). Time series from well-mixed systems like lakes document that these indicators give considerable warning in advance of regime shifts (e.g. Scheffer et al. 2009; Carpenter et al. 2011; Seekell et al. 2012; Batt et al. 2013). However, time series indicators can fail in systems with strong spatial connections, such as vegetated systems in arid regions where the diameters of root systems and canopies create distance dependent facilitation-competition relationships (D'Odorico et al. 2007; Dakos et al. 2011). Analyses of simulated data from stochastic ecosystem models suggest that spatial analogs for leading indicators of regime shifts (i.e. spatial variance and spatial autocorrelation) perform better in these types of spatially extended systems (Guttal and Jayaprakash 2009; Donangelo et al. 2010; Dakos et al. 2010). Additionally, because they gain power from sampling multiple points in space, spatial indicators are more practical than temporal indicators in that they require significantly fewer observations to detect change (Guttal and Jayaprakash 2009; Dakos et al. 2010; Dakos et al. 2011). As a consequence, there is a substantial interest in developing spatial analogs for temporal regime shift indicators (Kefi et al. 2014).

We previously presented tests for conditional heteroskedasticity as a leading indicator of regime shifts in ecological time series (Seekell et al. 2011; Dakos et al. 2012; Seekell et al. 2012). Conditional heteroskedasticity is clustered variance that is exhibited in ecosystems approaching a regime shift (Seekell et al. 2011; Seekell et al. 2012). Tests for conditional heteroskedasticity have been effective indicators of impending regime shifts when applied to simulated data from a variety of stochastic ecosystem models

(Seekell et al. 2011; Dakos et al. 2012) and were a highly effective indicator in a whole-ecosystem regime shift experiment designed to test the efficacy of leading indicators at spatial and temporal scales relevant to management (Seekell et al. 2012). Despite this success, an analogous technique for spatial data has not been evaluated. Here, we describe a test for spatial heteroskedasticity adapted for use as a leading indicator of desertification and evaluate its efficacy using data simulated from two spatially extended models of vegetation dynamics in arid regions.

Methods

Test for spatial heteroskedasticity

Tests for conditional heteroskedasticity in time series are calculated using a two-step process: 1) the data are filtered through an autoregressive time series model and then 2) a regression is used to test for autocorrelation among the squares of the filtered values (Seekell et al. 2011). Ord and Getis (2012) describe an analogous test for gridded spatial data: 1) each cell is filtered by subtracting the mean of adjacent cells, and then 2) spatial autocorrelation is assessed for the squares of the filtered data. Here, we assess clustering in the squares of the filtered data by applying Moran’s I index of spatial autocorrelation. Other metrics of spatial autocorrelation could be used (e.g. Ord and Getis 2012), but we used Moran’s I because 1) it is widely used by ecologists and 2) Moran’s I can be easily expressed as a regression, similar to the tests typically used to assess conditional heteroskedasticity in time series (Anselin et al. 1996; Fortin and Dale 2005; Anselin et al. 2006; Seekell et al. 2011).

Leading indicators such as spatial autocorrelation and spatial variance derive from the concept of critical slowing down – a condition when dynamical systems take progressively longer to recover from perturbations as they approach a bifurcation point (Wissel 1984; van Nes and Scheffer 2007; Dakos et al. 2010). Spatial heteroskedasticity is not directly related to critical slowing down, but rather responds to clustering of spatial variability (Ord and Getis 2012). Local variability is low for bare cells surrounded by bare cells (or vegetated cells surrounded by vegetated cells), but is high at the boundary of vegetated and vegetated areas. In semi-arid regions, vegetation can form distinct spatial patterns ranging from complete or near complete cover to labyrinth patterns and patches close to the transition to desertification (Rietkerk et al. 2002; Borgogno et al. 2009). We expect that as the vegetation patterns change, local variability due to edges will become increasingly clustered as patches of vegetation become smaller and edges between vegetated and bare areas contract (cf. Couteron 2002). Spatial heteroskedasticity should increase in response to these changes.

Analysis

We evaluated spatial heteroskedasticity as a leading indicator of desertification using data simulated on 100 × 100 grids from two spatially extended vegetation models (Dakos et al 2011). The first dataset was simulated from a stochastic ecohydrology model comprising the relationships between plant biomass, soil water, and surface water (Rietkerk et al. 2002). In this model, a spatial feedback operates in a way that leads to increased soil moisture near a plant and decreased soil moisture away from the plant. This scale dependent feedback creates patterns of regular vegetation patches which change in predictable as the ecosystem approaches the regime shift to desert (Rietkerk et al. 2002). The second dataset was simulated from a stochastic cellular automaton model where the probability of cells becoming vegetated increases if a neighboring cell is vegetated (Kefi et al. 2007b). This local facilitation dynamic creates scale-free vegetation patterns with patches of vegetation progressively breaking to smaller pieces up to a point where none of them is sustained and the ecosystem shifts to a desert (Kefi et al. 2007b). Dakos et al. (2011) give detailed descriptions of the models and parameterizations used.

The specific data used in our analyses were previously analyzed for testing the relative efficacies of spatial and temporal indicators of regime shifts in signaling desertification (Dakos et al. 2011). The data represent snapshots, similar to what one would get from repeated flyovers for remotely sensed imagery as a system degrades from vegetated to desert (Dakos et al. 2011). We use these data to compare spatial heteroskedasticity tests directly to spatial autocorrelation. Both spatial heteroskedasticity and spatial autocorrelation are assessed using the Moran's I statistic. For our analysis we calculated Moran's I for both spatial autocorrelation and spatial heteroskedasticity using a binary first order Queen contiguity spatial connectivity matrix. This creates an autocorrelation analysis that assesses the similarity of each grid cell to the average value of adjacent cells. This analysis is analogous to calculating lag-one autocorrelation in time series. The matrix of spatial connections (a cell is connected to its adjacent cells and disconnected to all other cells) was row standardized (so that row sums equal unity) prior to calculating Moran's I (Anselin 1996). We conducted this analysis for both datasets using the freeware application GeoDa (Anselin et al. 2006).

The scale-free vegetation model gives binary occupancy data (vegetated or bare). Prior to assessing spatial autocorrelation on this data, we applied a coarse-graining procedure to make the data quantitative (Dakos et al 2011). The coarse-graining procedure sums the values of 5x5 cell sub-matrices to create a new data matrix with a smaller number of larger (in terms of area) cells. We did not use the coarse-graining procedure prior to testing for spatial heteroskedasticity because spatial heteroskedasticity includes its own filtering step that creates continuous data from the binary values by subtracting the averages of adjacent cells from each cell value (see above; Ord and Getis 2012).

Most analyses of leading indicators are based on simulated data have long lead-up times to transitions (e.g. Seekell et al. 2011; Batt et al. 2013). However, in practice, long-term monitoring programs are difficult to maintain and monitoring may begin at different times relative to an impending regime shift and this may influence the magnitude and direction of trends (cf. Easterling and Wehner 2009). To test how this may influence interpretation of spatial autocorrelation and spatial heteroskedasticity, we evaluated trends in these indicators using Kendall's tau correlation coefficient beginning at different points in time (referred to as snapshots). If the direction and magnitude of trends were consistent among starting points, managers would draw the same conclusions about changes in ecosystem resilience regardless of when monitoring began. However, if there is variability in the direction and magnitude of trends, the start date for monitoring may influence the conclusions managers draw about changes in ecosystem resilience.

Results

Spatial patterns in data from the scale-dependent feedback model shifted from complete plant cover, to labyrinths, and then to patches as the system lost resilience and degraded to a desert state (Figure 1A, darker green cells are more heavily vegetated and light green cells are lightly vegetated or bare). The squared residuals of the simulated vegetation data after filtering had many of the characteristics of the simulated vegetated data (e.g. spotted and labyrinth patterns; Figure 1B). However, there is a key difference in that the centers of the spots and labyrinths have low values (light blue) as opposed to the raw data where the centers are high values (dark blue). For the scale-free model, plant cover decreased and became increasing patchy as the vegetation system approached the transition to the desert state (Figure 2A). After coarse-graining, the same pattern is evidenced but much of the fine scale pattern is smoothed over (Figure 2B). The squared residuals of the simulated vegetation data after filtering became increasingly clustered as the simulated system degraded (Figure 2C). The centers of patches have in the filtered data had low values (light blue) such that high variability edges (dark blue) draw closer as the patch sizes decrease.

For the system with scale-dependent dynamics, spatial autocorrelation was moderate when the system was mostly vegetated but jumped to high levels when patterning appeared (Figure 3A). After this initial jump, spatial autocorrelation declined slightly. When completely vegetated, spatial heteroskedasticity was near zero because of the few edges between vegetated and bare regions. Spatial heteroskedasticity increased consistently as the system degraded and the edges between vegetated and bare areas grew closer together (Figure 3A).

For the system with scale free dynamics, spatial autocorrelation generally increased as the system degraded, but with considerable variability (Figure 3B). This variability originates from the coarse-graining procedure that smoothed over cell-to-cell covariance in vegetation dynamics. When completely vegetated, spatial heteroskedasticity was near zero because of there are few edges between vegetated and bare regions. Spatial heteroskedasticity increased consistently as the system degraded (Figure 3B). Because the spatial heteroskedasticity analysis does not require coarse-graining, the cell-to-cell covariance is not smoothed over and the increase in spatial heteroskedasticity as the system degrades has considerably less variability then spatial autocorrelation.

For the scale dependent data, there is a weak positive trend overall in spatial autocorrelation (Figure 4A). However, this trend becomes negative if observations begin after the first snapshot. The lack of monotonic trend indicates that conclusions drawn from monitoring will depend on when a manager begins monitoring the system. For spatial heteroskedasticity, Kendall's tau was consistently at or near unity for each potential starting point, indicating that the increase in spatial heteroskedasticity was consistent throughout the course of degradation (Figure 4A). If a manager were to assess spatial heteroskedasticity, they would come to the same conclusion about declining resilience in the system, regardless of when monitoring began. For spatial autocorrelation in the scale-free data, trends were always positive but generally weaker (lower values of Kendall's tau) than trends in spatial heteroskedasticity. However, the trends did become strong for the last three snapshots (Figure 4B). For spatial heteroskedasticity, Kendall's tau was at or near unity for all possible starting points for assessing trends, indicating that managers would draw the same conclusions from the analysis regardless of the starting point for monitoring (Figure 4B).

Discussion

Spatial heteroskedasticity increased consistently prior to desertification in simulated arid systems exhibiting scale-free and regular pattern formation. Spatial heteroskedasticity increased sooner and more consistently than spatial autocorrelation. Hence, spatial heteroskedasticity appeared more reliable than spatial autocorrelation as a leading indicator of regime shifts in such simulated patterned data. Temporal tests for conditional heteroskedasticity require long uninterrupted time series (e.g. 50-200 time steps; Seekell et al. 2011; Seekell et al. 2012), but spatial heteroskedasticity tests required only a handful of time steps (e.g. < 10) and these time steps do not have to be equally spaced. The characteristics of spatial heteroskedasticity as a leading indicator are well suited for terrestrial vegetated systems where the temporal scale of dynamics are long (at least relative to the fast dynamics of microbial systems and phytoplankton in lakes where many temporal leading indicators have been tested, see Carpenter et al. 2011; Seekell et al. 2012; Dai et al. 2012) and it may be impractical to wait and collect data for a large amount of time before beginning to assess leading indicators of regime shift (i.e. a shift may happen in the time it takes to collect enough data to calculate the temporal indicator only once).

We did not include metrics of statistical significance in our spatial heteroskedasticity analysis. We experimented with a randomization approach (e.g. Kefi et al. 2014), but because spatial data easily achieve large sample sizes, even the most trivial values of Moran's I are significantly different from zero. For instance, Moran's I for spatial heteroskedasticity in the least degraded snapshot of the scale-dependent data was 0.021, but was highly significant ($p = 0.001$) because the sample size was $n = 10{,}000$.

This hypersensitivity is common for spatial indicators (Kefi et al. 2014). We experimented with reducing sample sizes and found that it improves the efficacy of randomization tests for the spatial heteroskedasticity such that there is not significant heteroskedasticity in stable systems, and significant heteroskedasticity in degrading systems. However, we also found with smaller sample sizes that the spatial heteroskedasticity test will not respond strongly if the smaller extent of the image does not fully encompass the spatial patterning.

For large sample sizes, the spatial heteroskedasticity statistic should be evaluated by the dual criteria of a value greater than zero (there is no concept of negative autocorrelation heteroskedasticity, see Seekell et al. 2012) and strong positive trend. This type of dual criteria may not be possible for spatial autocorrelation or spatial variance because natural scale-dependent processes that create vegetation patterns also create non-monotonic trends in spatial indicators in systems with declining resilience (D'Odorico et al. 2006; Dakos et al. 2011). This is in part because changes in vegetation patterns are not unique to systems with critical slowing down (D'Odorico et al. 2006; Borgogno et al. 2009). Hence the dual criteria are unique to spatial heteroskedasticity tests and represent an advantage for interpretation.

Because spatial heteroskedasticity responds strongly to edges, spatial heteroskedasticity tests will not respond to declining resilience in systems where there is no pattern formation. In cases where diffusion does not allow the emergence of patterns, spatial autocorrelation or spatial variance may be better indicators (e.g. Guttal and Jayaprakash 2009; Dakos et al. 2011). This property is not unique to spatial heteroskedasticity - other powerful indicators such as discrete Fourier transformations also respond weakly in systems lacking pattern formation (Carpenter and Brock 2010; Kefi et al. 2014). However, in both aquatic and terrestrial systems, diffusion only dominates spatial connections at very small scales. The distance dependent relationships that dominate at scales relevant to ecosystem management form spatial patterns to which the spatial heteroskedasticity test should respond (Abraham 1998; Borgogno et al. 2009). Hence, indicators like spatial autocorrelation may outperform spatial heteroskedasticity at small scales, but may perform less well in assessing larger scale dynamics.

Heterogeneity in ecosystem processes is well studied, especially at the landscape scale (e.g., Dutilleul and Legendre 1993; Pickett and Cadenasso 1995). However, relatively little is known about the pervasiveness of heteroskedasticity in records of ecosystem properties (Seekell et al. 2011; Seekell et al. 2013). Our results suggest that spatial heteroskedasticity could be a useful leading indicator of desertification in arid systems. Field tests will be crucial to further developing this and other spatial indicators at scales relevant to understanding ecosystem regime shifts and for ecosystem management (Seekell et al. 2011; Bestelmeyer et al. 2013; Kefi et al. 2014).

Acknowledgements

DAS is supported by the United States National Science Foundation, the Virginia Space Grant Consortium, and the University of Virginia Department of Environmental Sciences. VD is supported by a Marie Curie fellowship and a Rubicon grant. Michael Pace provided helpful comments.

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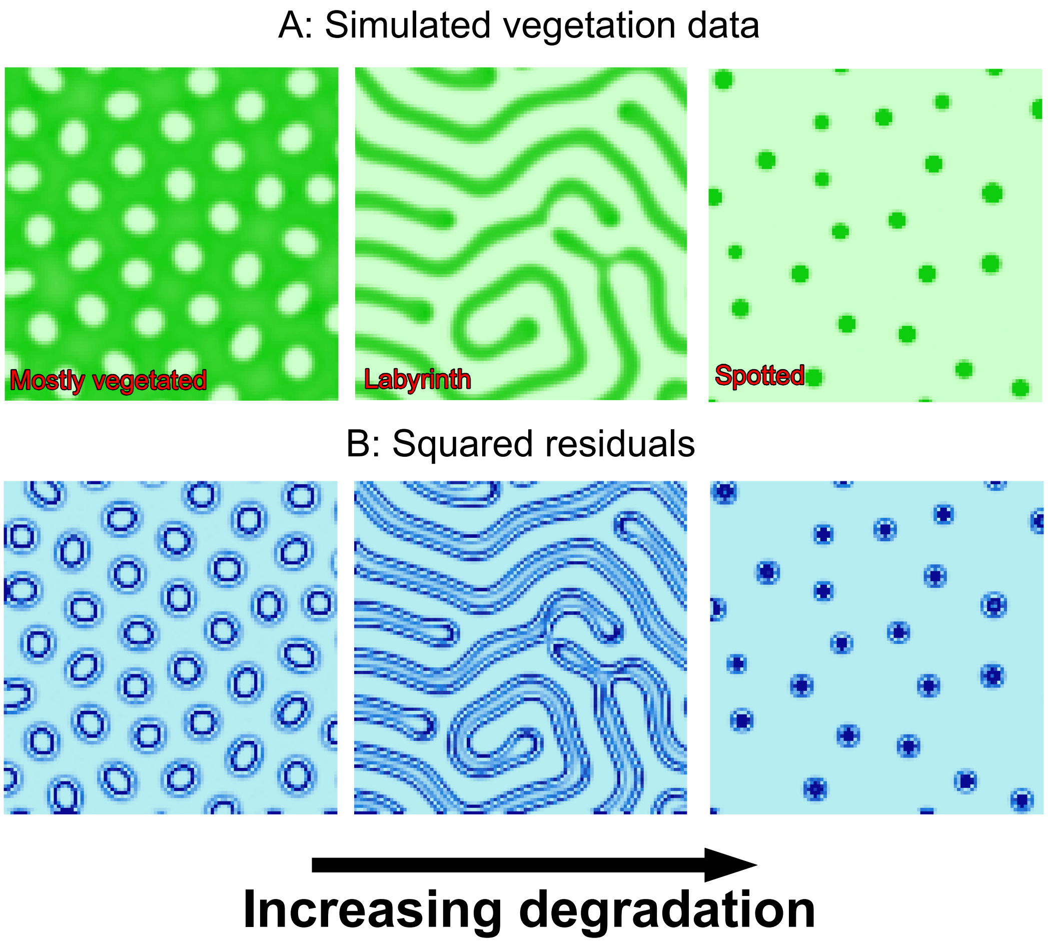

Figure 1. A: Three example snapshots of simulated data from the scale-dependent vegetation model. Darker shades correspond to higher values. B: The squared residuals for three snapshots of simulated data from the scale-dependent vegetation model, after filtering.

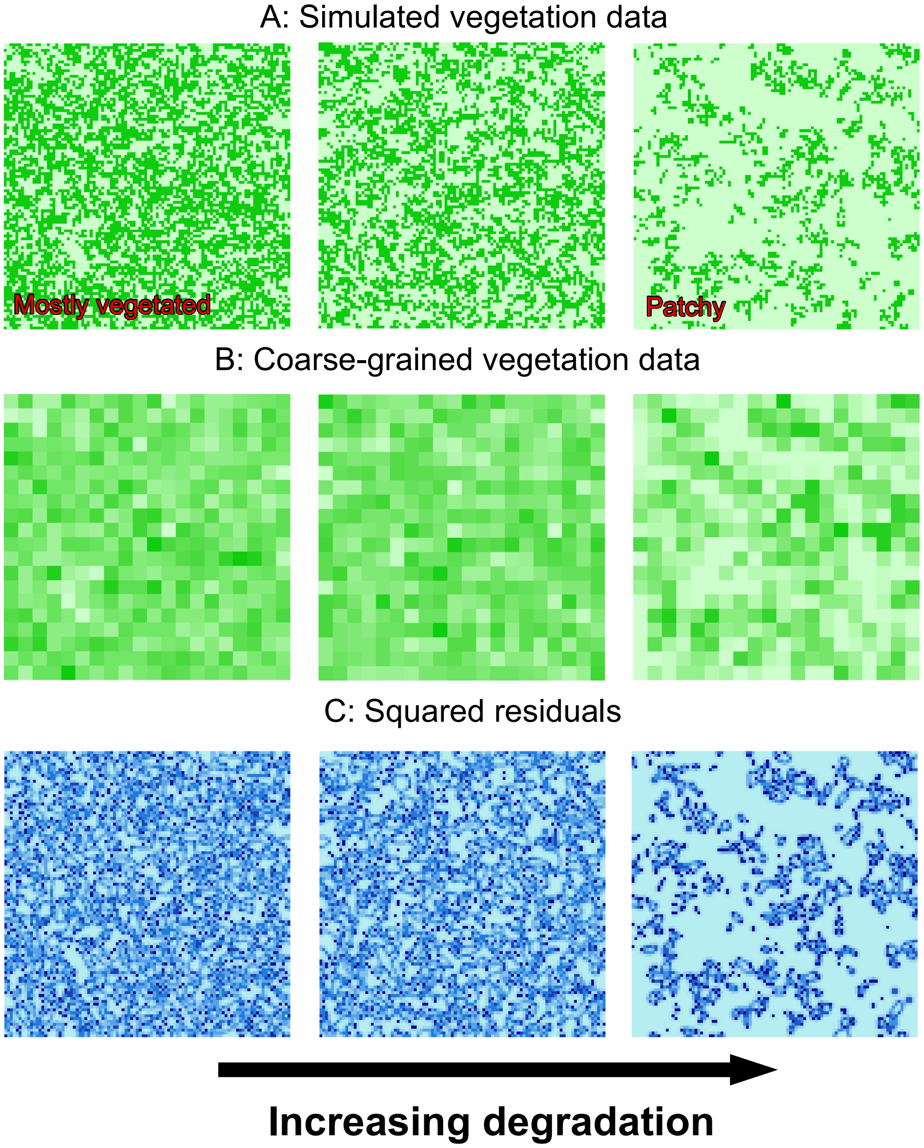

Figure 2. A: Three snapshots of simulated data from the scale-free vegetation model. The data are binary (i.e. 0 if a cell is not vegetated, 1 is a cell if vegetated). Dark cells are vegetated and light cells are bare. B: Three snapshots of the simulated data after a coarse-graining procedure transforms the binary data into continuous values. C: The squared residuals for three snapshots of simulated data from the scale-free vegetation model, after filtering. Application of the filter eliminates the need for coarse-graining procedures before assessing spatial heteroskedasticity.

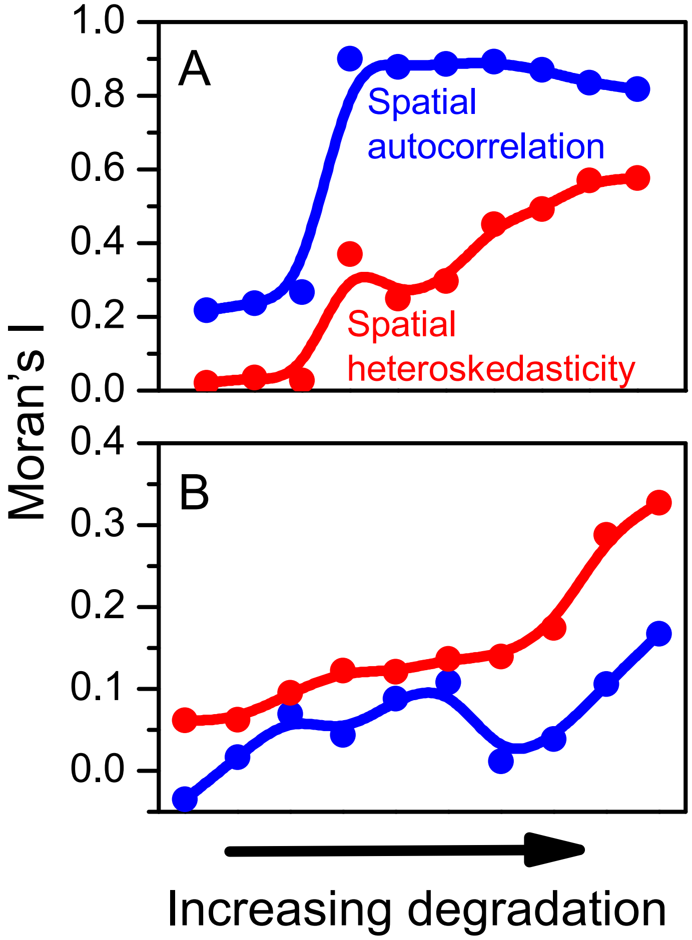

Figure 3. A: Moran's I statistics for spatial autocorrelation and spatial heteroskedasticity applied to ten snapshots of simulated vegetation data from the spatially explicit model with scale-dependent dynamics. B: Moran's I statistics for spatial autocorrelation and spatial heteroskedasticity applied to ten snapshots of simulated vegetation data from the spatially explicit model with scale-free dynamics. For both panels, B-splines are fit to the data to emphasize patterns.

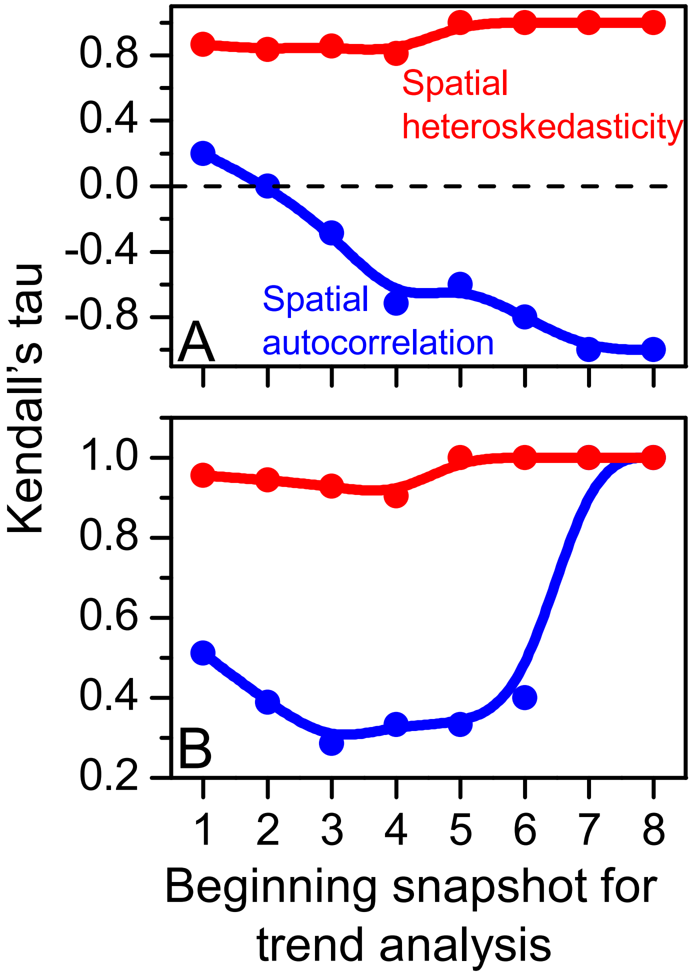

Figure 4. Kendall's tau correlation coefficients assessing the magnitude and direction of trends with different starting points. The first point (furthest left) is the trend in indicator values across all ten snapshots. Each point to the right represents the trend beginning with a later snapshot (i.e. the furthest right point is the trend in indicators across only the last three snapshots in time). A: Results from the vegetation model with scale-dependent patterns. B: Results from the vegetation model with scale-free patterns. For both panels, B-splines are fit to the data to emphasize patterns.

CHAPTER 4: EVIDENCE OF ALTERNATE ATTRACTORS FROM A WHOLE-ECOSYSTEM REGIME SHFIT EXPERIMENT[3]

Abstract

Ecosystems sometimes shift between different states or dynamic regimes. Theory attributes these shifts to multiple ecosystem attractors. However, documenting multiple ecosystem attractors is difficult, particularly at spatial and temporal scales relevant to ecosystem management. We manipulated the fish community of a lake with the goal of causing trophic cascades and shifting the food web from a planktivore-dominated state to an alternate piscivore-dominated state. We evaluated evidence that the shifts in the fish community comprise alternate attractors using two complementary approaches. First, we calculated phase space trajectories to visualize the shift between attractors. Second, we computed generalized autoregressive conditional heteroskedasticity (GARCH) models and the Brock-Dechert-Scheinkman (BDS) test for linearity. The reconstructed phase space trajectories show the system departing a point attractor, entering a limit cycle, and then shifting to a new point attractor. The GARCH and BDS results indicate that linear explanations are not sufficient to explain the observed patterns. The results provide evidence for alternate attractors based on high-frequency time series of field measurements.

Introduction

Ecosystems sometimes shift between different states or dynamic regimes (Scheffer et al. 2001; Scheffer and Carpenter 2003). For example, savannas shift to

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[3] Seekell DA, Cline TJ, Carpenter SR, Pace ML (2013) Evidence of alternate attractors from a whole-ecosystem regime shifts experiment. Theoretical Ecology 6:385-394.

deserts, lakes shift from clear water to algae blooms, and fisheries shift from thriving to collapsed (Scheffer et al. 2001). These shifts are sometimes attributed to shifts among multiple attractors (Holling 1973; Scheffer and Carpenter 2003). Multiple attractors potentially explain sudden, dramatic ecosystem changes as well as failures to predict or reverse unwanted changes (Scheffer et al. 2001; Scheffer and Carpenter 2003; Suding et al. 2004). However, empirical tests for the existence of multiple ecosystem attractors are difficult and consistent evidence remains elusive (e.g., Carpenter and Pace 1997; Scheffer et al. 2003; Schröder et al. 2005; Mittelbach et al. 2006; Persson et al. 2007; Hobbs et al. 2012; Schröder et al. 2012). Laboratory experiments on model systems document multiple attractors (e.g., Fussmann et al. 2000; Dai et al. 2012), but complex patterns and variability in field data have led to disagreement over the existence and importance of multiple attractors in ecosystems (e.g., Carpenter 2001; Biesner et al. 2003; Hsieh et al. 2005; Mittelbach et al. 2006; Mumby et al. 2007; Hsieh et al. 2008; Bruno et al. 2009).

Evidence for existence of multiple ecosystem attractors comes from several types of studies in a variety of systems (Scheffer and Carpenter 2003). For example, Scheffer et al. (2003) found that drainage ditches demonstrating floating or submerged plant dominance exhibited bimodality and path dependency (when slightly different initial conditions lead to very different ending conditions), both characteristics of a system with more than one attractor (see also Scheffer and Carpenter 2003; Schröder et al. 2005; de Young et al. 2008; Andersen et al. 2009). In other studies, tests for discontinuous response to changing environmental conditions, path dependency, lack of recovery from perturbations, and changes in driver–response relationships are often used to infer alternative attractors (see reviews by Scheffer and Carpenter 2003, and Schröder et al.

2005). These tests are often coupled to ecosystem models with multiple attractors that exhibit the same patterns (e.g., Scheffer et al. 2003; see review by Schröder et al. 2005). The strong empirical evidence from laboratory experiments (Schröder et al. 2005) proves the potential for multiple attractors in ecological systems. In field settings statistical comparisons of mechanistic models with and without alternative attractors have proven a powerful means of testing for multiple attractors in ecosystems when long-term data are available (Carpenter and Pace 1997; Carpenter 2003; Scheffer and Carpenter 2003; Mumby et al. 2007; Ives et al. 2008; Schooler et al. 2011). Thus, the consistency of models and data in long-term observational studies represents the primary evidence for multiple attractors in ecosystems.

The existence of multiple attractors is due to certain non-linear processes (Scheffer et al. 2001; Scheffer and Carpenter 2003). However, combinations of linear processes not associated with multiple attractors can also cause shifts in means, bimodality, and changes in driver-response relationships similar to those observed in systems with alternate attractors (Scheffer and Carpenter 2003; Schröder et al. 2005; Scheffer et al. 2003; Hsieh et al. 2005; Daily et al. 2012; Dakos et al. 2012). While patterns such as path dependency, bimodality, and hysteresis are indicative of two or more attractors, these patterns do not reconstruct attractors themselves. Physicists and economists have developed statistical tests and visualization techniques for identification of non-linear dynamics and shifts between multiple attractors in time series. For instance, tests for linearity can be applied to time series data to evaluate linear dynamical hypotheses (e.g., Brock et al. 1991; Brock et al. 1996; Hsieh et al. 2005). If linear possibilities are eliminated then nonlinear explanations are more plausible (Brock et al.

1991; Brock et al. 1996). In other approaches, lagged values from time series can be plotted in certain combinations to visualize the form of attractors in phase space (Takens 1981; Schaffer 1984). These approaches make no *a priori* assumptions about ecological processes and are promising for detecting multiple attractors in ecosystems when other approaches are difficult to apply or interpret. Nonetheless these visualization and statistical approaches are not widely used (Hsieh et al. 2005; Sugihara et al. 2012).

Application of novel techniques such as tests for linearity and phase space reconstructions has been identified as a priority in efforts to evaluate multiple attractors, particularly at spatial and temporal scales relevant to ecosystems (Scheffer and Carpenter 2003; Hsieh et al. 2005). We previously reported a whole-ecosystem experiment where we manipulated the fish community in a small lake with the purpose of testing for early warning indicators of a regime shift (Carpenter et al. 2011; Seekell et al. 2012; Pace et al. 2013). Here, we use a unique 4-year high-resolution time series derived from this experiment to test the hypothesis that this change comprised a shift between two alternate attractors. We examine phase plots for patterns consistent with a transition between two attractors and test for bursts of variance not explained by linear time series models, which should accompany a transition between attractors.

Background and Theory

We manipulated Peter Lake, a small (area: 2.6 ha; max depth: 19.6 m) oligotrophic lake in the Upper Peninsula of Michigan (89°32' W, 46°13' N). The lake was minnow dominated from 1991 onward due to earlier experiments that removed much of a predatory largemouth bass *Micropterus salmoides* population (Carpenter et al. 2001). By the time of the present study began, the prey fish community consisted of a mixture of minnows including golden shiner *Notemigonus crysoleucas*, fathead minnow *Pimephales promelas*, dace *Phoxinus* spp., brook stickleback *Culaea inconstans*, central mudminnow *Umbra limi* and pumpkinseed *Lepomis gibbosus*. These small fishes dominated Peter Lake and there was only a small population of predatory adult (> 150 mm) largemouth bass (Carpenter et al. 2011). The minnow dominance prior to the experiment was maintained because large numbers of prey fish suppress growth of juvenile largemouth bass, increasing juvenile largemouth bass vulnerability to predation or other stressors and thereby preventing growth and recruitment of juveniles into the adult largemouth bass population (Walters and Kitchell 2001; Carpenter et al. 2008; Carpenter et al. 2011).

We expected that slowly adding adult largemouth bass would shift the food web from minnow dominance to largemouth bass dominance. We hypothesized that if the abundance of adult predators increased past a critical point, adult predators would dramatically reduce the prey population (Carpenter et al. 2008). The resulting reduction in competition should allow juvenile predators to grow and subsequently recruit into the adult population. The feedback maintaining minnow dominance (minnows cause a recruitment bottleneck for largemouth bass) consequently shifts to a feedback maintaining largemouth bass dominance (largemouth bass continue suppressing minnows such that their juveniles can continue recruiting into the adult population, causing further suppression of the minnows).

Our expectations for the existence of alternate ecosystem attractors in this system and the ability of largemouth bass additions to shift the system between alternate attractors derive from a mathematical model of the Peter Lake food web, which was solved to show that altering largemouth bass abundance creates multiple ecosystem attractors (see Carpenter et al. 2008). The specific ecological mechanism for the alternate attractors is the existence of trophic triangles – a set of predator–prey relationships where positive feedbacks can drive either predators or prey to dominance – in fish communities, including the Peter Lake fish community (Walters and Kitchell 2001; Carpenter 2003; Carpenter et al. 2008; Carpenter and Scheffer 2009).

A shift between alternate attractors due to nonlinear dynamics is not the only possible mechanism for change due to largemouth bass additions (Carpenter et al. 2011). For instance, largemouth bass additions could cause step-change reductions in minnow abundance without changing feedbacks within the food web. This would happen if, for example, sudden increases adult largemouth bass simply forced minnows into short-term refuges without eliminating the largemouth bass recruitment bottleneck. Such a change could be intrinsically linear and not associated with alternate ecosystem attractors. Previous fish community manipulations in this and nearby lakes did not attempt to discriminate between linear and nonlinear dynamics and these previous studies were based on low-frequency time series suitable for linear analyses but unsuitable for statistical tests to reject linear dynamics (He et al. 1993; Carpenter et al. 2001). In the present analysis, we leverage high-frequency measurements to discriminate between these linear and nonlinear possibilities.

Methods

Food web manipulation

We added 1,200 golden shiners on 28 May 2008 to help prevent the transition to largemouth bass dominance from happening too quickly to be detected by early warning statistics applied in our previous analyses (Carpenter et al. 2011). The number of fish added was < 10% of the existing minnow population (Carpenter et al. 2011). Subsequently, we slowly added adult largemouth bass to Peter Lake over the course of four summers (12 on 7 July 2008, 15 on 18 June 2009, 15 on 21 July 2009) to cause trophic cascades and create a transition from a state of prey dominance to predator dominance. The system stabilized in its new condition toward the end of 2010. However, we added additional largemouth bass in 2011 (32 on 23 June 2011) to ensure that the food web structure would not revert due to winterkill, which may occasionally happen in this lake, after the study was complete (Hodgson and Kitchell 1987).

By experimentally increasing the population of adult largemouth bass we attempted to push the system from a minnow dominated point attractor, through a zone of bi-stability, to a new largemouth bass dominated point attractor (Carpenter et al. 2008). This design is different than some tests for alternate attractors that induce transitions in experimental systems from one attractor to another within the zone of bistability and with no structural change in the system, then monitor the system for several generations to evaluate persistence at the new attractor (Dudgeon et al. 2010). In other words, our manipulation is not designed to shift the system between attractors within a zone of bistability, but is meant to create structural changes in the system by manipulating a slow moving variable (Walker et al. 2012). This mechanism is consistent with mathematical understanding of multiple ecosystem attractors and is also thought to represent the principal mechanism of change between alternate attractors in ecosystems (Scheffer et al. 2001; Scheffer and Carpenter 2003; Fauchald 2010).

Sampling

We measured prey fish abundance daily with 30 minnow traps (6mm mesh with two 25mm openings) spaced approximately equidistant around the perimeter of the lake. All trapped fish were released back into the lake at their capture location. The average number of prey fish caught per trap per day for each summer was concatenated into one time series (cf. Carpenter 1993). The resulting time series was log transformed and differenced once prior to the statistical analysis to ensure normality of time series model (see below) residuals. We only sampled from late May to early September but concatenating these time series is unlikely to affect our analysis because our sampling period encompassed the dominant ecological processes relevant to this study. Further, there were no obvious jumps between years that would suggest dramatic overwinter changes in fish abundance that might adversely affect the statistical analysis (Fig. 1, see also Appendix 2).

Statistical analysis

Aggregates of linear processes may cause changes in the mean or variance of a time series and these changes can be mistaken for nonlinear structure by statistical tests for linearity. Time series models commonly applied to ecological data, such as autoregressive moving average models, filter linear structure from the mean, but the residuals could contain linear structures from the error variance that could be mistaken for hidden nonlinear structure. Consequently, we filtered the data through a generalized autoregressive conditional heteroskedasticity (GARCH) time series model (Bollerslev

1986). GARCH models remove linear relationships from the time series by predicting mean values and error variances based on linear terms (Bollerselev 1986; Hsieh 1991). Structure in the residuals of such models is likely due to nonlinear processes affecting either the mean or the variance that are not removed by the GARCH model. We fit the models using maximum likelihood in an approach that is typical for application of GARCH models. This approach is described in detail in Appendix 2. We standardized the residuals from the GARCH model by dividing by the conditional variance (Hsieh 1991). We plotted ecosystem phase space trajectories based on the standardized GARCH residuals to identify the form of the nonlinear relationship. Ecosystem trajectories for standardized GARCH residuals are created by plotting in three dimensions a state variable $x(\mathrm{t})$ by $x(\mathrm{t}+T)$ by $x[\mathrm{t}+(m-1)T]$, where m is an embedding dimension and T is a time lag (Schaffer 1984). The resulting plot contains the dynamical properties of the system and the patterns formed are diagnostic of different types of nonlinear dynamics and attractors (Takens 1981; Schaffer 1984). Some types of stochastic variation may alter the nature of nonlinear dynamics and a limitation of plotting the ecosystem trajectories is that the lagged variables approach is not designed to handle this (Horsthemke and Lefever 1984). However, the noise in this system is thought to be additive (see Carpenter et al. 2008) and while this type of noise may cause variability in phase plots such that it is more difficult to discern patterns, additive noise should not alter the underlying dynamics recovered in the plot. To minimize these effects, we smoothed the standardized GARCH residuals using a seven point moving average and plotted the resulting trajectories as B-splines (cf. Schaffer 1984). We also created phase plots in the original state space of the data (i.e. using unfiltered data) for comparison. We display each phase plot in two dimensions for ease of viewing. For each plot, the X (*x*(t)) and Z (*x*[t+(*m*-1)*T*]) axis are the abscissa and ordinate, respectively. Each phase plot uses an embedding dimension $m = 2$ and lag $T = 3$.

We tested the standardized residuals for departure from being independent and identically distributed (IID) using the Brock-Dechert-Scheinkman (BDS) test (Brock et al. 1991; Brock et al. 1996; see Lai 1996, Carpenter et al. 2011, and Dakos et al. 2012 for applications of the BDS test in ecological contexts). The standardized GARCH residuals are independent and identically distributed (IID) if linear processes determine the ecosystem dynamics (Hsieh 1991). For some nonlinear processes, including the ones we are interested in, the standardized GARCH residuals are not IID (Hsieh 1991; Dakos et al. 2012). The BDS test can be thought as a statistical test for spatial correlation of time series histories in phase space (Brock et al. 1991; Brock et al. 1996). After GARCH filtering, linear dynamics will create a random pattern in phase space whereas nonlinear dynamics will be patterned (correlated) in phase space (Brock et al. 1991; Schaffer 1984). The GARCH model can approximate and remove some nonlinear dynamics (Engle 1982, Granger 1991). Hence in our application, the BDS test applied to the standardized GARCH residuals is a conservative way to screen out linear mechanisms that could otherwise appear to be nonlinear dynamics (Granger 1991; Brock et al. 1996; Dakos et al. 2012). We calculated probability values for the BDS test by bootstrapping ($n = 10{,}000$ permutations) the standardized GARCH residuals (Brock et al. 1996; Carpenter et al. 2011). We did not use asymptotic probability values for the BDS test because they deviate considerably from the normal distribution if the GARCH model is not correctly specified (Brock et al. 1991; Brooks and Heravi 1999). The bootstrapped probability values are robust to potential misspecification errors (Brock et al. 1991).

The BDS test has two free parameters, the embedding dimension and the radius, used to determine if the history of points in the system trajectory are near each other in phase space. We calculated the BDS test with a variety of embedding dimensions and radius parameters because there is no theoretically optimal parameter choice (Brock et al. 1991; Hsieh 1991; Brock et al. 1996). Significant BDS tests for a wide variety of combinations of embedding dimensions and radii indicate a robust conclusion (i.e. indicating non-linear vs. linear dynamics). We applied the BDS test instead of other tests (e.g., the S-map procedure used by Hsieh et al. 2005) because BDS is well vetted and has good power for a variety of types of dynamics (Hsieh 1991; Brock et al. 1991). Other linearity tests (e.g., S-map or Tsay's test; see Hsieh et al. 2005 and Tsay 1986, respectively) may be more powerful than the BDS test for certain narrowly-specified hypotheses, but we do not assume one type of dynamic *a priori* and hence a more general test is appropriate for our application (Brock et al. 1991; Brooks and Henry 2000).

The two approaches we apply to identify alternate attractors are complementary. The phase space plots are the main results of the analysis and represent a unique case where a transition between ecosystem attractors can be visualized in phase space. The BDS test is a supporting result that does not identify alternate attractors directly, but rules out spurious linear explanations for the patterns observed in the phase plots.

Results

Prior to the first largemouth bass addition to Peter Lake, small prey fishes were abundant based on trap catches and there was high day-to-day variability (Fig. 1, top panel). After the first largemouth bass addition, catches immediately declined. Variability shifted to lower frequencies – meaning from high day-to-day variability to longer-term oscillations. By the time of the last largemouth bass addition, daily catches were low and stable (Fig. 1, top panel).

The standardized GARCH residuals are displayed in the bottom panel of Figure 1 (gray line). Tabular results from the model selection procedure and parameter values of the best fitting GARCH model used to produce the residuals are given in Appendix 2. The smoothed values (red line) are steady before and after the first and last largemouth bass additions, consistent with linear dynamics at a point attractor. However, there are oscillations during the transition between point attractors (the time between the first and last largemouth bass addition), indicating that the oscillations in the unfiltered catch time series are likely due to non-linear dynamics. The oscillations in the standardized GARCH residuals are of approximately the same amplitude, suggestive of limit cycle dynamics. There were no oscillations prior to the first largemouth bass addition that would suggest nonlinearity due to the early golden shiner addition. The bootstrap BDS test applied to the raw (gray line, bottom panel Figure 1) standardized GARCH residuals was significant over a wide range of parameter values. Twenty-one of twenty-four tests were significant at the 0.05 level of significance and two additional tests were significant at the 0.1 level. Only one BDS test was not significant. The large number of tests with low probability values, especially considering that the BDS test is conservative when applied to GARCH residuals (Granger 1991; Brock et al. 1996), indicates that the oscillations in standardized GARCH residuals cannot be explained by linear processes and can plausibly be attributed to nonlinear dynamics such as those associated with alternate attractors (Table 1).

Figure 2 is the phase portrait for the Peter Lake minnow trap time series prior to GARCH filtering. The line represents the trajectory of the prey fish community over time as it moves to different parts of the phase space. The mean catch declines during the study and the system dynamics change as the mean catch does. The blue portion of the line is the system varying around an attractor, prior to the first largemouth bass addition. The gray line is the trajectory during the transition period (between the first and last largemouth bass additions). The circular pattern is consistent with the fish entering into a limit cycle (May 1972). The red line is the trajectory during the period after the last largemouth bass addition. There is considerably less variability after the transition period than before the transition.

Figure 3 is the phase portrait for the Peter Lake minnow trap time series based on standardized GARCH residuals. The same basic dynamics are present as in the raw data, but the form of the attractors is clearer. Prior to the first largemouth bass addition (blue portion of the trajectory), the system is varying around a point attractor. The system has some excursions away from the attractor towards the upper right quadrant of the figure, but the trajectory returns around the same point attractor. The transition period (grey portion of the trajectory) retains its circular pattern consistent with a limit cycle dynamic. After the transition period (red line portion of the trajectory) the system varies around a point attractor with some excursions to the bottom left quadrant. The magnitude of variability around the two point attractors is much more similar in the phase plot based on standardized GARCH residuals (Fig. 3) than in the phase plot based on the raw data (Fig. 2).

The two point attractors in Figure 3 appear to overlap in phase space. This is because the figures are drawn from standardized GARCH residuals, which are centered on zero. Hence the two point attractors are centered at zero. To clarify the dynamics and emphasize that these are unique point attractors, we re-plotted the trajectories before and after the first and last largemouth bass additions with vectors for each point in time to denote the direction of the system trajectory (Figure 4). The trajectory during the transition period is excluded for clarity. These vectors show the trajectories almost always returning to the point attractors. However, when there are large excursions, the trajectories before the first and after the last largemouth bass addition "spin" back to the attractors in opposite directions (Figure 4), indicating that the attractors are unique even though they overlap in phase space.

Discussion

Our analysis provides evidence of two point attractors in a food web. The system began oscillating and this transition began soon after the first largemouth bass addition. These oscillations continued for two years until the system converged to a new, predator-dominated attractor. The BDS test ruled out linear explanations for these patterns suggesting that the manipulation represents a true nonlinear regime shift between alternative attractors.

The transitional dynamics were due to the interaction of fast and slow ecological processes. Largemouth bass abundance is a slow changing variable (Walker et al. 2012), driven by our experimental additions and the annual reproductive cycles of this species. Minnow catch is a fast changing variable where large magnitude intra-annual variability is driven by behavior, specifically the decisions to move between foraging zones and refuges as well as shoaling in response to predation risk (Carpenter et al. 2011). We interpret the oscillations in our analysis as resulting from delays due to annual reproductive cycles. The largemouth bass had a large year class in 2009 and direct and indirect predation risk suppressed competition from minnows such that many of these young-of-year largemouth bass survived through the winter into 2010 (cf. Post et al. 1998). The juvenile largemouth bass grew rapidly and were able to prey on small minnows midway through 2010. The largemouth bass spawned again in 2010 and the system was pushed out of an oscillatory phase to the largemouth bass dominated point attractor. The extended delay between annual reproductive cycles of largemouth bass allowed time for cycles to form in minnow dynamics due to behavior. Eventually, largemouth bass dominance suppressed minnow cycles as the system settled to the alternate attractor.

Recent theoretical and field studies have identified early warning signals such as increased variance and increased autocorrelation that occur in ecological time series prior to shifts between alternate attractors (van Nes and Scheffer 2007; Carpenter et al. 2008; Scheffer et al. 2009; Carpenter et al. 2011). Autocorrelation and variance will often increase together prior to a critical transition between alternate attractors driven by a slow variable (Brock and Carpenter 2012), but these indicators do not increase simultaneously if noise perturbs the system from one attractor to another or if there is no shift between attractors (Ditlevsen and Johnsen 2010; Wang et al. 2012). The indicators will also not respond to step changes in control variables, for instance if the largemouth bass additions suddenly pushed the system to a new attractor without allowing for changes in internal feedback mechanisms (Carpenter et al. 2011). We previously reported increased variance and autocorrelation in chlorophyll-a concentration and zooplankton biomass prior to a suspected shift between alternate attractors in this experiment (Carpenter et al 2011; Seekell et al. 2012; Pace et al. 2013). These increases occurred during the transition period and dissipated after the shift between attractors. The early warning indicators provide strong corroborating evidence of the nonlinear dynamics identified in our present analysis because variance and autocorrelation would not have increased simultaneously if the food web had not shifted from one attractor to another or if the transition was caused by a strong perturbation and not our experimental manipulation. Further, these indicators would not have returned to low levels after the transition if the system remained in an unstable condition as opposed to converging to a new attractor.

How long will the system persist in the predator dominated state? This is difficult to predict. Some shifts between attractors are essentially permanent, at least at time scales relevant to humans (e.g., desertification; species extinctions), but others are not (e.g., trophic cascades). While we cannot predict with certainty how long the system will stay in the predator dominated state, we do know that it is possible for largemouth bass dominated states to persist for long periods. For instance, an adjacent lake (Paul Lake) has been dominated by largemouth bass for at least thirty years (Carpenter et al. 2001). Peter Lake had a similar largemouth bass dominated fish community prior to 1991 and this suggests that a largemouth bass dominated state in Peter Lake could also persist for an extended period of time (Carpenter et al. 2001). However, largemouth bass are cannibalistic and this can lead to large oscillations in adult largemouth bass abundance over time. For instance, in Paul Lake, adult largemouth bass populations vary by five fold in eight to ten year cycles (Post et al. 1998). If the largemouth bass in Peter Lake enter into cyclical population dynamics, the probability of a sudden reverse transition will increase during the minima of these cycles, when stochastic events (such as winterkills) might push the largemouth bass population below the critical threshold for dominance, causing a reverse transition to small fish dominance (Rosenzweig 1971). Hence while the predator-prey role reversal associated with the transition between point attractors occurred very rapidly in this study (relative to the lifespan of the organisms: ~10 years for largemouth bass), the longer term dynamics are not clear and will depend both on the life history of the fish (the ability to develop strong cohort dynamics) and on the occurrence of strong random shocks to the system. In addition, the small fish populations in Peter Lake were not driven to extinction during the four years of this study but may be in the longer term. Under such conditions, piscivore dominance might be more sustained and less subject to reversal to the alternate attractor of small fish dominance.

Our analytical approach is well suited for identifying the existence of alternate attractors in ecosystems. However, our approach is unable to resolve some parallel problems that are particularly relevant for ecosystem management. For instance, we are unable to calculate a threshold value for the transition between states from our analysis. Environmental stochasticity creates a range of possible transitions depending on the magnitude of perturbations and hence it is difficult to know what the critical point will be prior to reaching it (Guttal and Jayaprakash 2007). We are also unable to calculate the probability that the transition is or is not reversible through management (Carpenter and Lathrop 2008). These questions are probably best addressed with a correctly specified mechanistic model of the system. Despite this limitation, confirmation of the existence of alternate ecosystem states has profound management implications because the ability to switch between states is known, even if thresholds are unknown (Carpenter et al. 1999; Carpenter 2001; Peterson et al. 2003).

The magnitude and variability in phase space trajectories was different between the standardized GARCH residuals and the raw minnow trap catch time series (compare Figures 2 and 3). There is much more variability in the raw data in the period prior to the transition than in the period after the transition. This is because mean catch is tightly correlated with the variance and skewness of the distribution of catch (cf. Seekell 2011; Seekell et al. 2011). The high variance at the first attractor in the raw data is a function of the inherent high variability when fish catch is high. Likewise, the low variability at the second attractor is because there is inherently low variability when mean catch is low. This high and low variability is not due to the regime shift but rather the decline in minnow populations resulting from increased predator abundance. These changes in variability are not present in the phase plot for standardized GARCH residuals (Figure 3). For standardized GARCH residuals, the two attractors have similar variability because the GARCH model removed changes in variance due to linear dynamics (i.e. due simply to reduced size of minnow populations caused by the predator additions). Further, the magnitude of variability during the transition is greater than the variability around the attractors in Figure 3. This is consistent with theoretical expectations for lake food webs (see Carpenter et al. 2008), indicating that the GARCH filtering isolated non-linear dynamics associated with the regime shift (i.e. the results are not simply due to a linear reduction in prey due to predator additions).

The significant GARCH terms in our model indicate time-varying variance. While the application of GARCH models is extremely common in some disciplines (e.g.

economics), we know of no prior applications to ecological data. Hence it is difficult to known the prevalence and potential implications of GARCH type processes in ecosystems. The GARCH dynamics in this system are consistent with a system approaching a transition between alternate attractors (Seekell et al. 2011; Seekell et al. 2012). GARCH dynamics in stable systems could provide false positive early warnings of transitions between ecosystem attractors. However, GARCH dynamics are not typically present in models of stable ecosystems (Seekell et al. 2011). Further, the significance of BDS tests here in and our previous analyses (see Carpenter et al. 2011) indicate potential nonlinearities beyond GARCH processes and this is consistent with expectations for early warning indicators (Carpenter et al. 2011; Dakos et al. 2012). Further application of these types of models to ecological data is necessary to better understand the prevalence of GARCH dynamics in ecosystems.

The potential for transition between point attractors is widely discussed in ecology but the evidence for and approaches to detecting these attractors in ecosystems have been disputed (e.g., Connell and Sousa 1983; Sutherland 1990; Scheffer and Carpenter 2003; Schröder et al. 2005; Dudgeon et al. 2010). Tests for hallmark patterns of alternate attractors such as hysteresis, path dependence, and bimodality have provided evidence for the existence of alternate attractors in a wide variety of systems including laboratory model systems, oceans, lakes, and forests, at a variety of scales – from competition between two species (e.g., between floating and submerged vegetation, Scheffer et al. 2003) to huge changes in regional structure (e.g., collapse of Saharan vegetation between 5000 and 6000 years ago, deMenocal et al. 2000, Scheffer and Carpenter 2003). However, these results are often based on observational records and a review of experimental tests for alternative attractors by Schröder et al. (2005) revealed that ecosystem-scale studies and studies involving long-lived organisms such as fish typically do not find evidence of alternative attractors. This has led concern over the generality of the concept of alternative attractors (Schröder et al. 2005). For instance, there is disagreement over the applicability of the concept of alternative states to the highly visible and dramatic shift from hard coral to algal dominance in Caribbean coral reefs where ecosystem scale experiments are difficult or impossible to conduct and long-term data is both rare and potentially confounded by changing baseline conditions (Mumby et al. 2007; Dudgeon et al. 2010). Our result relative to alternate attractors is specific to the fish community dynamics in one lake analyzed in this study, but is a consequence of relatively general ecosystem phenomena (trophic triangles, trophic cascades). Our results show empirically that alternate attractors can exist at the ecosystem scale and that these attractors can be reconstructed and evaluated from high-resolution time series.

Acknowledgements

This work was supported by the National Science Foundation (DEB 0716869, DEB 0917696, and the Graduate Research Fellowship Program) and University of Virginia Department of Environmental Sciences. We thank William Brock for helpful discussions and Jonathan Cole and two anonymous reviewers for providing comments on the manuscript. We thank R. Batt, C. Brosseau, J. Coloso, M. Dougherty, A. Farrell, J. Hodgson, R. Johnson, J. Kitchell, S. Klobucar, J. Kurtzweil, K. Lee, T. Matthys, K. McDonnell, H. Pack, L. Smith, T. Walsworth, B. Weidel, G. Wilkinson, C. Yang, and L.

Zinn for technical help in the laboratory and field.

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Table 1. Probability values from bootstrapped ($n = 10{,}000$) BDS tests on the standardized GARCH residuals. We experimented with a variety of radiuses ($\varepsilon = 0.25–2 \times \sigma$, where σ is the standard deviation of the standardized GARCH residuals) and embedding dimensions ($m = 2–5$).

ε			$m = 2$	$m = 3$	$m = 4$	$m = 5$
$0.25 \times \sigma$	=	0.858	0.0079	0.0046	0.0057	0.0053
$0.50 \times \sigma$	=	1.716	0.0041	0.0007	0.0004	0.0002
$0.75 \times \sigma$	=	2.574	0.0031	0.0017	0.0002	0.0000
$1.00 \times \sigma$	=	3.433	0.0117	0.0056	0.0061	0.0059
$1.50 \times \sigma$	=	5.149	0.1025	0.0127	0.0093	0.0089
$2.00 \times \sigma$	=	6.865	0.4064	0.0733	0.0203	0.0146

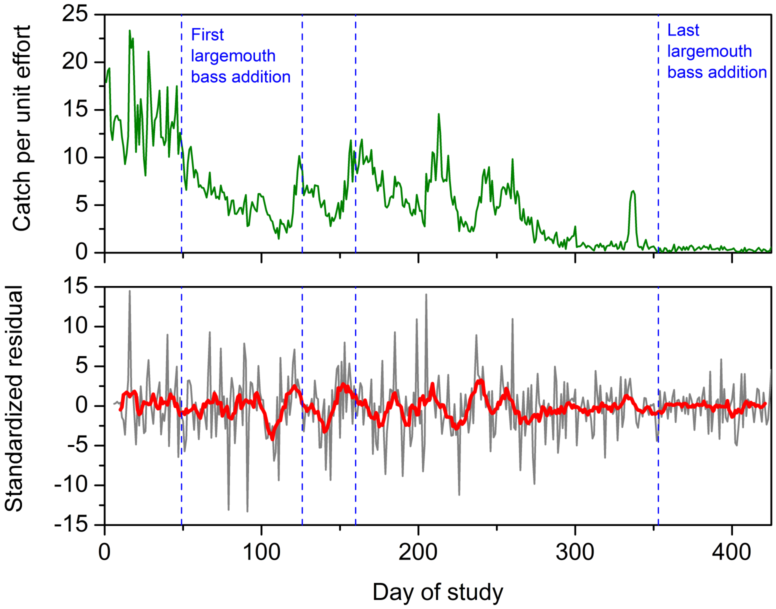

Figure 1. Top: Mean catch per day for minnow traps in the manipulation lake for four summers (11 May – 27 August 2008; 18 May – 4 September 2009; 17 May – 3 September 2010; 16 May – 3 September 2011). The largemouth bass additions are denoted with dashed vertical blue lines. We consider the time before the first addition and after the last addition to be stable. The time between these additions is considered the transition. Bottom: The gray line is the time series of standardized residuals from the GARCH time series model fit to the mean catch-per-day time series. The red line is the standardized residuals smoothed using a seven point moving average.

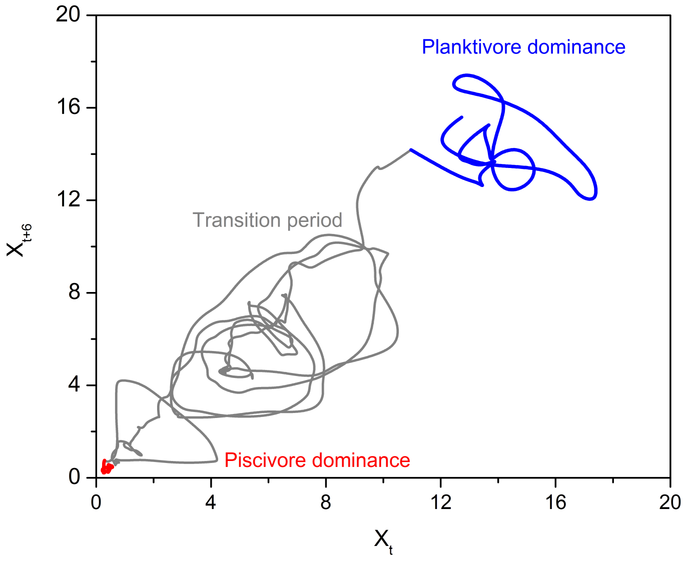

Figure 2. Phase space plot of the Peter Lake minnow trap time series (untransformed and unfiltered). The blue trajectory is the period prior to the first largemouth bass addition. The gray trajectory is the transition period. The red trajectory is the period after the last largemouth bass addition. The system is initially at a point attractor, but enters into a limit cycle after the first largemouth bass addition. The system has returned to a new point attractor by the time of the last largemouth bass addition.

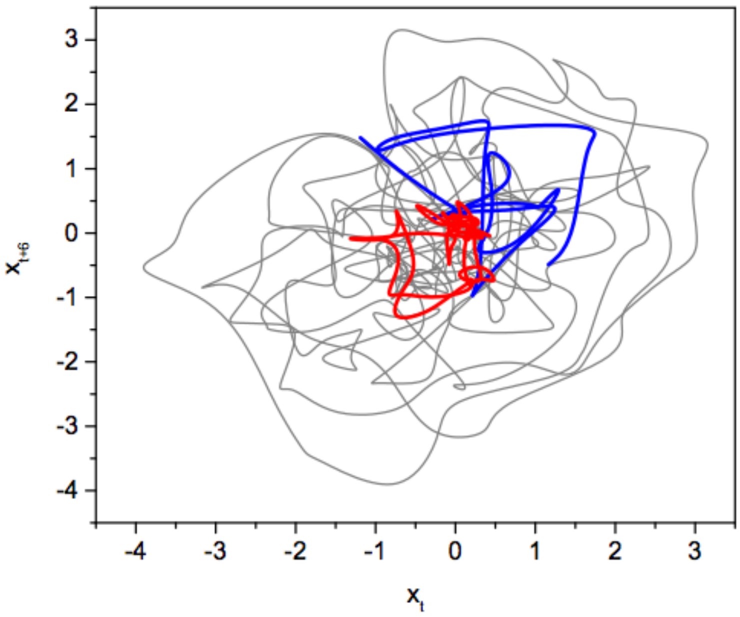

Figure 3. Phase space plot of standardized GARCH residuals for the Peter Lake minnow trap time series. The blue trajectory is the period prior to the first largemouth bass addition. The gray trajectory is the transition period. The red trajectory is the period after the last largemouth bass addition. The system is initially at a point attractor, but enters into a limit cycle after the first largemouth bass addition. The system has returned to a new point attractor by the time of the last largemouth bass addition. The two point attractors appear very close to each other because they are based on the standardized GARCH residuals that are centered at zero.

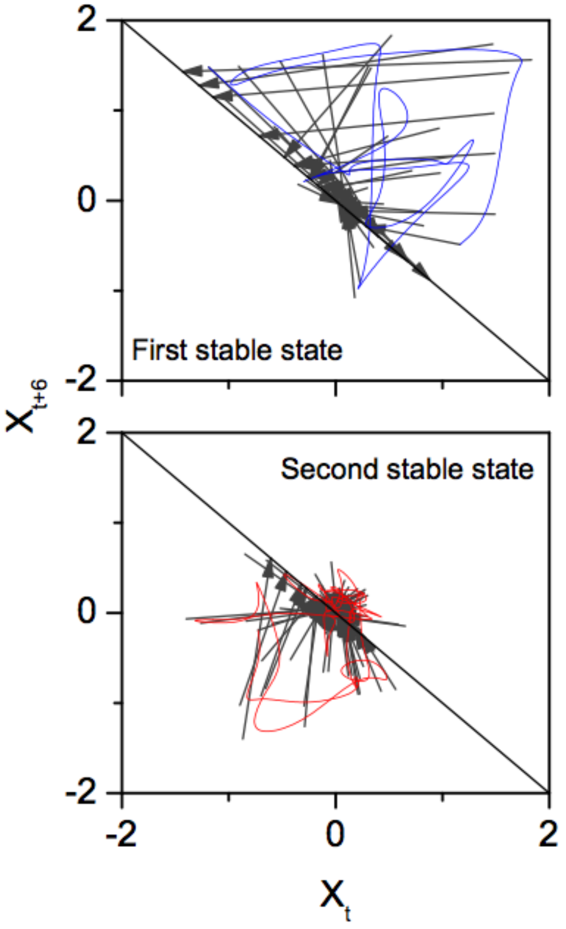

Figure 4. Vector plots for the manipulation lake minnow trap time series trajectories before the first (top) and after the last (bottom) largemouth bass additions when the manipulation lake varied around point attractors. The point attractors appear close to each other because the time series are center around zero. However, the system diverts and varies around these states in different directions, indicating that they are distinct.

CHAPTER 5: CONDITIONAL HETEROSKEDASTICITY FORECASTS REGIME SHIFT IN A WHOLE-ECOSYSTEM EXPERIMENT[4]

Abstract

Regime shifts in stochastic ecosystem models are often preceded by early warning signals such as increased variance and increased autocorrelation in time series. There is considerable theoretical support for early warning signals, but there is a critical lack of field observations to test the efficacy of early warning signals at spatial and temporal scales relevant for ecosystem management. Conditional heteroskedasticity is persistent periods of high and low variance that may be a powerful leading indicator of regime shift. We evaluated conditional heteroskedasticity as an early warning indicator by applying moving-window conditional heteroskedasticity tests to time series of chlorophyll-*a* and fish catches derived from a whole-lake experiment designed to create a regime shift. There was significant conditional heteroskedasticity at least a year prior to the regime shift in the manipulated lake but there was no significant conditional heteroskedasticity in an adjacent reference lake. Conditional heteroskedasticity was an effective leading indicator of regime shift for the ecosystem manipulation.

Introduction

Statistical anomalies in time series, such as increased variance and increased autocorrelation, are early warning indicators of ecosystem regime shifts (Scheffer and others 2009). The statistical properties of early warning indicators are well established by theoretical and simulation studies (e.g., Carpenter and Brock 2006, van Nes and Scheffer

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[4] Seekell DA, Carpenter SR, Cline TJ, Pace ML (2012) Conditional heteroskedasticity forecasts regime shift in a whole-ecosystem experiment. Ecosystems 15:741-747.

2007, Guttal and Jayaprakash 2008). However, there are a variety of problems associated with detecting early warnings of regime shifts in real systems including large noise disturbances, observation errors, confounding trends in external perturbations, small sample sizes, and unknown mechanisms causing regime shifts. These difficulties are typically minimized when simulated data are used to test early warning theory (Carpenter 2003 Scheffer and others 2009, Seekell and others 2011). Consequently, the efficacy of early warning indicators is unresolved, because there is a critical lack of field-testing for early warning indicators, particularly at spatial and temporal scales relevant to ecosystem managers.

Conditional heteroskedasticity is persistent error variance in time series models that appears as clustered volatility (Engle 1982). This type of variance is a powerful leading indicator of regime shifts in modeled systems (Seekell and others 2011). Conditional heteroskedasticity is present when variance at one time step is dependent on variance at the previous time step. Periods of high variance follow periods of high variance and periods of low variance follow periods of low variance. Variance in stable ecosystems is typically constant, but increases prior to a regime shift (Carpenter and Brock 2006, Scheffer and others 2009). This pattern suggests conditional heteroskedasticity as an early warning indicator because the portion of a time series near an impending shift will appear as a cluster of high volatility while portions of the time series further away from the regime shift will appear as clusters of low volatility (Seekell and others 2011). Thus there should be conditional heteroskedasticity in ecological time series prior to a regime shift, but no conditional heteroskedasticity in ecological time series without a regime shift (Seekell and others 2011).

Early warning indicators that are based on interpreting statistical patterns (e.g. high versus low variance) may detect an impending regime shift when there is none (Scheffer and others 2009, Seekell and others 2011, Appendix 3). Such false positives could result in expensive and unnecessary management action. Conditional heteroskedasticity tests are easily associated with probability values (Engle 1982, Engle and others 1985). Probability values minimize false positives by providing cut-offs for evaluating when an early warning signal is meaningful (Seekell and others 2011, Appendix 3).

We previously documented a whole-ecosystem experimental regime shift where top predators were added to a lake to cause trophic cascades and to shift the ecosystem from dominance by planktivorous fish to dominance by piscivorous fish (Carpenter and others 2011). Trophic cascades are a common type of non-linear ecosystem regime shift, and the strong responses in system components such as phytoplankton biomass provide an opportunity for evaluating new early warning indicators (Pace and others 1999, Carpenter and others 2008, Carpenter and others 2011). Here, we evaluate conditional heteroskedasticity as a leading indicator of ecological regime shift. We use existing data from the previously documented experimental regime shift reported by Carpenter and others (2011), as well as an additional year of data acquired after that report. The purpose of our analysis was to evaluate the practicality of conditional heteroskedasticity as an early indicator using a known regime shift with high frequency data at scales relevant to ecosystem managers. We test if conditional heteroskedasticity provides early warnings well in advance of the regime shift and if these tests minimize false warnings when there is no impending regime shift.

Methods

Regime shift manipulation—Carpenter and others (2011) conducted a food web manipulation on Peter Lake using a second system (Paul Lake) with similar morphometry and chemistry as a reference. Prior to their experiment, Peter Lake was dominated by pumpkinseed sunfish *Lepomis gibbosus*, a variety of other small species of fish, and few adult (> 150 mm) largemouth bass *Micropterus salmoides*. Paul Lake was dominated by adult largemouth bass with a small population of pumpkinseed. The food-webs represent alternative stable structures of similar species composition with the consequence of piscivore dominance in Paul Lake and planktivore dominance in Peter Lake. Prior to the manipulation, Carpenter and others (2011) re-enforced the initial state of planktivore dominance in Peter Lake by adding 5,000 golden shiners *Notemigonus crysoleucas* on 28 May 2008. Peter Lake was manipulated over four summers (2008–2011) by adding adult largemouth bass to shift the lake to a state of piscivore dominance, similar to the reference system. Because the threshold population of largemouth bass required to fully transition the system to piscivore dominance was unknown, adult largemouth bass were added slowly (12 adult largemouth bass on 7 July 2008, 15 adult largemouth bass on 18 June 2009, and 15 adult largemouth bass on 21 July of 2009) to maximize the potential to test for early warning indicators. In response to the manipulation, the abundance of small fishes declined, zooplankton size structure shifted to larger body-sized forms, and phytoplankton biomass declined (Carpenter and others 2011). Largemouth bass produced a large year class in 2009 and many of these offspring survived the following winter to recruit into the adult largemouth bass population in 2010. This recruitment indicates the transition from planktivore to piscivores dominance in the fish community. Turbulence from this transition cascaded through the lower part of the food web until the latter part of 2010 when the entire transition was complete or nearly so. The lake stabilized in this new condition in 2011 and an additional 32 adult largemouth bass were added on 23 June 2011 to re-enforce the piscivore-dominated state. Conditions in the reference lake did not change during the study. The results of the first three years of the manipulation, documented by Carpenter and others (2011), were consistent with the hypothesis that disruption of the food-web would lead to increased variance, increased autocorrelation, critical slowing down (i.e. slower recovery from perturbations), increased skewness, non-linearity, and shifts to increased low frequency variance of key indicator variables prior to the regime shift. The results of the fourth year of the study were consistent with the manipulation system stabilizing at a new regime including decreased variance and autocorrelation (Appendix 3).

We applied conditional heteroskedasticity tests to chlorophyll-*a* time series derived from this experiment because previous theoretical and empirical work suggested chlorophyll-*a* concentration, a measure of phytoplankton biomass, strongly reflects early warning signals of regime shifts driven by trophic cascades (Carpenter and others 2008, Carpenter and others 2011). Chlorophyll-*a* was determined daily in the mixed layer of both lakes (for each lake n = 105 in 2008, n = 110 in 2009, n = 110 in 2010, n = 110 in 2011) between mid-May and early September over four years. To measure chlorophyll-*a*, we took 200 mL water samples from a depth of 0.5 m from each lake and filtered the samples onto glass fiber filters. The filters were frozen and chlorophyll-*a* was subsequently extracted in methanol and measured with a fluorometer according to Holm-

Hansen and Riemann (1978).

We also applied conditional heteroskedasticity tests to minnow trap catch time series derived from the experiment. Changes in minnow trap catch time series are driven by both changes in biomass and fish behavior. Previous theoretical and empirical work suggested that these times series display non-linear dynamics and early warning signals of regime shifts driven by trophic cascades (Carpenter and Kitchell 1993, Carpenter and others 2008, Carpenter and others 2011). Thirty minnow traps were deployed in the littoral zone of Peter Lake and twenty minnow traps were deployed in the littoral zone of Paul Lake from late May to early September during the four study years. The traps (6mm mesh with two 25mm trap openings) were monitored daily (Peter Lake n = 96 in 2008, n = 108 in 2009, n = 110 in 2010, n = 111 in 2011; Paul Lake n = 95 in 2008, n = 108 in 2009, n = 110 in 2010, n = 111 in 2011) and the abundance of each species of fish collected in each trap was recorded. Time series were derived from these data by calculating the average catch per trap in each lake for each day.

Statistical analysis—A rolling window Lagrange multiplier test for conditional heteroskedasticity was applied to the time series for each lake (Engle 1982, Engle and others 1985, Seekell and others 2011). Rolling windows are based on calculating the early warning indicator for all observations (n) from n_t to $n_{t\text{-}wl}$ where t equals time intervals (days in our study) and wl equals window length. The calculation is iterated for each day with the result being a rolling series of conditional heteroskedasticity tests. We used a 50-day window length in this study because this was a good trade-off between statistical power (larger window widths correspond to higher statistical power) and preserving a large number of windows necessary to make meaningful interpretations of changes in indicator values and to precisely delimitate transitions (smaller window widths correspond to a larger number of windows and more precise delimitation of the timing of transitions). The Lagrange multiplier test for conditional heteroskedasticity is calculated by:

1) Fitting a time series model to the data
2) Squaring the residuals of the time series model
3) Regressing the squared residuals on themselves, lagged one time step
4) If the slope of the regression in step three is > 0, multiply the multiple r^2 value from step 3 by the sample size in step 3. If the slope of the regression in step 3 is ≤ 0, there is no conditional heteroskedasticity. There is no concept of a negative slope in step 3.
5) Calculating a probability value by comparing the value obtained in step 4 with a Chi square distribution with one degree of freedom.

Worked examples of the conditional heteroskedasticity test are provided in Seekell and others (2011). For display, we plot the r^2 value from step 4 instead of the Lagrange multiplier test statistic. Because each window is the same width, a critical value to assess the significance of r^2 values is obtained by dividing the critical value from the chi-square distribution with one degree of freedom by the sample size of the auxiliary regression. We applied criteria of $p < 0.1$ as the critical probability of significance in this study.

Based on prior studies of ecological models, significant conditional heteroskedasticity tests indicate an impending regime shift while non-significant conditional heteroskedasticity tests do not indicate an impending regime shift (Seekell and others 2011). We expected no significant conditional heteroskedasticity in Paul Lake during the study. We expected no significant conditional heteroskedasticity in Peter Lake prior to the manipulation and significant conditional heteroskedasticity as trophic cascades created turbulence in the food web as the regime shift proceeded. Based on model analyses, conditional heteroskedasticity is expected to become non-significant quickly after a regime shift (see Seekell and others 2011).

For step 1 of the analysis we applied an auto-regressive lag-4 model ($y_t = b_0 + b_1 y_{t-1} + b_2 y_{t-2} + b_3 y_{t-3} + b_4 y_{t-4} + \varepsilon$) to the time series and the conditional heteroskedasticity tests to the residuals of these time series models. We selected a model with four autoregressive terms because in these lakes chlorophyll-a autocorrelation and minnow trap autocorrelation is only significant at ≤ 4 lags and the partial autocorrelation is generally only significant at ≤ 2 lags. Thus in most cases an autoregressive lag-4 model will over-fit data and such a time series model will contain more lags than necessary. Over fitting the number of autoregressive lags in the time series model will not cause the Lagrange multiplier test to perform more poorly than a correctly specified model and will actually improve performance if an important moving average term or covariate is omitted from the time series model (Lumsdaine and Ng 1999). Under fitting the time series model can adversely affect the performance of the conditional heteroskedasticity test by increasing chance of finding false positives.

Moving window conditional heteroskedasticity tests were robust to a range of window widths, time series models, and choices of threshold probability values for significance based on a sensitivity analysis (see Appendix 3).

Results

Chlorophyll-a time series—Prior to the manipulation (2008), Peter and Paul Lakes had similar chlorophyll-*a* concentrations (Fig. 1). Chlorophyll-*a* concentrations in Peter Lake were dynamic with substantial oscillations during the manipulation (2009 and 2010), while chlorophyll-*a* concentrations in Paul Lake were less variable (Fig. 1). The fourth year of data (2011), not previously reported, was collected using the same methods as the previous three years to ensure that Peter Lake had stabilized at the new piscivore dominated regime. Chlorophyll-*a* concentrations were low in Peter Lake and similar to Paul Lake during this year. The declining phase of spring blooms were observed in Peter Lake and perhaps in Paul Lake during the first two weeks of observations in 2008 and 2011.

There was no significant conditional heteroskedasticity ($p > 0.1$) in Paul Lake during the four-summer study based on the rolling window conditional heteroskedasticity analysis (Figure 2). There was also no significant conditional heteroskedasticity in Peter Lake in 2008 during the early phase of the manipulation. There was significant conditional heteroskedasticity ($p < 0.1$) in Peter Lake for almost all of 2009 and the first half of 2010. Conditional heteroskedasticity became non-significant during the second half of 2010, consistent with results given by Carpenter and others (2011), indicating that the shift in food-web structure to piscivore dominance had occurred. There was no significant conditional heteroskedasticity in Peter Lake during the final year (2011) after the regime shift was completed.

Minnow trap catch time series—Prior to the manipulation (2008), Peter Lake had high minnow trap catch and Paul Lake had very low minnow trap catch (Fig. 3). Minnow trap catch in Peter Lake declined after largemouth bass additions and became more variable during the manipulation (2009 and 2010). Minnow trap catches in Paul Lake were close to zero and were not variable (Fig. 3). Some of the oscillations in Peter Lake trap catches, at the beginning of the summers, may be associated with increased near shore activity due to pumpkinseed spawning. Oscillations later in the summer are not consistent with increased activity due to spawning. In the fourth year (2011), minnow abundance in Peter Lake stabilized near the levels observed in Paul Lake with the exception of an increase in near shore activity in Peter Lake due to spawning. This spawning activity was interrupted by a sudden shift to cold weather and hence the near shore activity (and high catches) was only sustained for a brief period of time.

There was significant conditional heteroskedasticity ($p < 0.1$) in Peter Lake in 2008 after largemouth bass additions began (Fig. 4). There was significant conditional heteroskedasticity ($p < 0.1$) for most of 2009 although there was not significant conditional heteroskedasticity ($p > 0.1$) for a period of time at the beginning of the summer when increased trap catch is likely due to spawning activity and not trophic cascades. There was no significant conditional heteroskedasticity ($p > 0.1$) in 2010 or 2011 with the exception of a brief period in 2011, which was due to the disruption of pumpkinseed spawning when a large and sudden shift in weather that drove pumpkinseeds off of their nests. There was no significant conditional heteroskedasticity in Paul Lake in 2008, 2009, or 2011 (Figure 4). There were two significant moving windows at the beginning of 2010, but no significant conditional heteroskedasticity during the remainder of the summer.

Discussion

Conditional heteroskedasticity was a powerful leading indicator that warned of the incipient regime shift about a year in advance. Conditional heteroskedasticity disappeared from the experimental system after the regime shift, indicating that the system arrived at a new stable state. In the chlorophyll-*a* time series there were no significant tests in the reference lake or in the manipulated lake in the year prior to and the year after the manipulation. In the minnow trap time series there were only two significant tests after the system had stabilized at the new state, and these significant tests were associated with a disrupted life history process (i.e. spawning). There were also only two significant tests in the reference system for the chlorophyll-*a* and minnow trap time series, combined. These results indicate that conditional heteroskedasticity provided early warning of the regime with minimal false positives.

Time series statistics used as early warning indicators of regime shift are subject to false positives. During the early part of 2008, there was increased chlorophyll-*a*, and this appears similar to the oscillations observed prior to the regime shift. This pattern also occurred in 2011 and we speculate the dynamics are the consequence of phytoplankton spring blooms. More complete monitoring of these blooms was not possible for this study because difficult or impassable road conditions in the early spring limit access to the study lakes. There were no significant conditional heteroskedasticity tests during these periods. However, such blooms could lead to false positives in other indicators. For instance, the high chlorophyll-*a* values associated with spring blooms are followed by low values and this could increase variance in a moving window analysis (e.g., Carpenter and others 2006, Carpenter and others 2011). Such increases in variance are consistent with an impending regime shift. The conditional heteroskedasticity test's probability values in this analysis aid interpretation by providing a baseline from which to judge the meaningfulness of indicator values.

Early warnings based on the conditional heteroskedasticity tests appeared first in the minnow trap time series. Significant tests were observed in the latter half of 2008 and for most of 2009. Significant conditional heteroskedasticity occurred in 2009 and 2010 for the chlorophyll-*a* times series. The earlier response associated with minnows reflects the effects of largemouth bass predation on both the abundance and behavior of these fish (Carpenter and others 2011). Upon introduction of piscivores, prey species quickly increase the occupancy of refuges and this shift in behavior contributes to trophic cascade effects (Carpenter and others 2010). The response of chlorophyll-*a* was more delayed and was the consequence of slower evolving shifts propagating through the food web (Carpenter and others 2011).

A recent review (Scheffer and others 2009) identified significance testing for early warning indicators as an important priority for research on this topic. Conditional heteroskedasticity tests provide a useful method for addressing this priority. An alternative approach to significance testing is to apply trend statistics, such as Kendall's tau, to early warning indicator values calculated from moving windows (Dakos and others 2008, Dakos and others 2010). A significant upward trend in moving window variance or autocorrelation estimates would be considered the early warning signal using this approach (e.g., Dakos and others 2008, Dakos and others 2010). However, moving window indicators are generally highly autocorrelated and trend statistics such as Kendall's tau are subject to increased false positives under these conditions (Hamed and Rao 1998). Conditional heteroskedasticity as an early warning indicator is based on a sequence of significance tests, each applied to the uncorrelated residuals of a time series filter. Hence, our analysis does not calculate significance values between windows and is not subject to this potential source of error. In other words, like all moving window indicators, the sequence of conditional heteroskedasticity tests is highly autocorrelated. However, the conditional heteroskedasticity significance tests are not based on these highly correlated moving windows. The significance test for trend statistics is based on these highly correlated moving windows.

In conclusion, based on our analysis of data from a whole-lake experiment, conditional heteroskedasticity is a powerful leading indicator of ecological regime shifts that is robust to false positives. These tests have simple (i.e. significant versus not significant) interpretations and were successfully applied to a system with natural environmental stochasticity with an unknown amount of observation error. Additional experience in applying the conditional heteroskedasticity approach is needed to further explore the sensitivity and robustness of these tests for a variety of regime shift conditions.

Acknowledgments

This work was supported by the National Science Foundation (DEB 0716869, DEB 0917696, and Graduate Research Fellowship Program) and University of Virginia Department of Environmental Sciences. We thank R. Batt, C. Brosseau, J. Cole, J. Coloso, M. Dougherty, A. Farrell, J. Hodgson, R. Johnson, J. Kitchell, S. Klobucar, J. Kurtzweil, K. Lee, T. Matthys, K. McDonnell, H. Pack, L. Smith, T. Walsworth, B. Weidel, G. Wilkinson, C. Yang, and L. Zinn for technical help in the laboratory and field.

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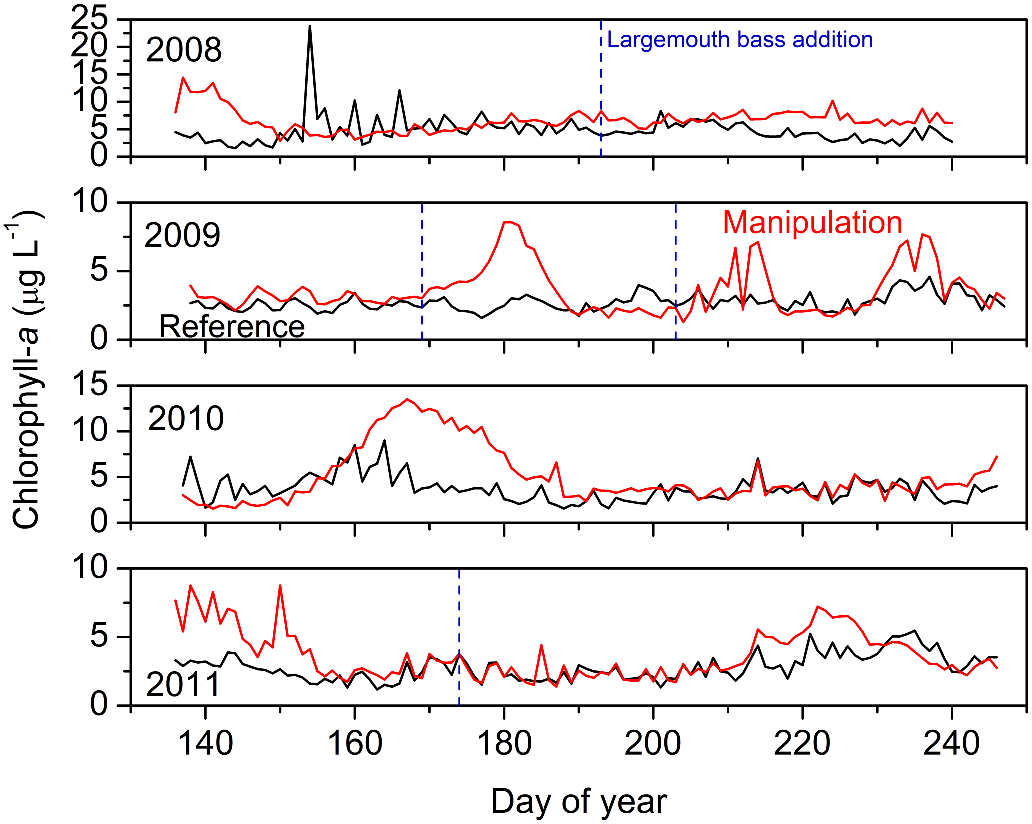

Figure 1. Daily chlorophyll-*a* measurements (μg L^{-1}) from the mixed layer of the manipulated Peter Lake (red) and reference Paul Lake (black) systems. Vertical dashed blue lines denote the timing of largemouth bass additions to the manipulated Peter Lake. Note the vertical axis scales are different between years for display purposes.

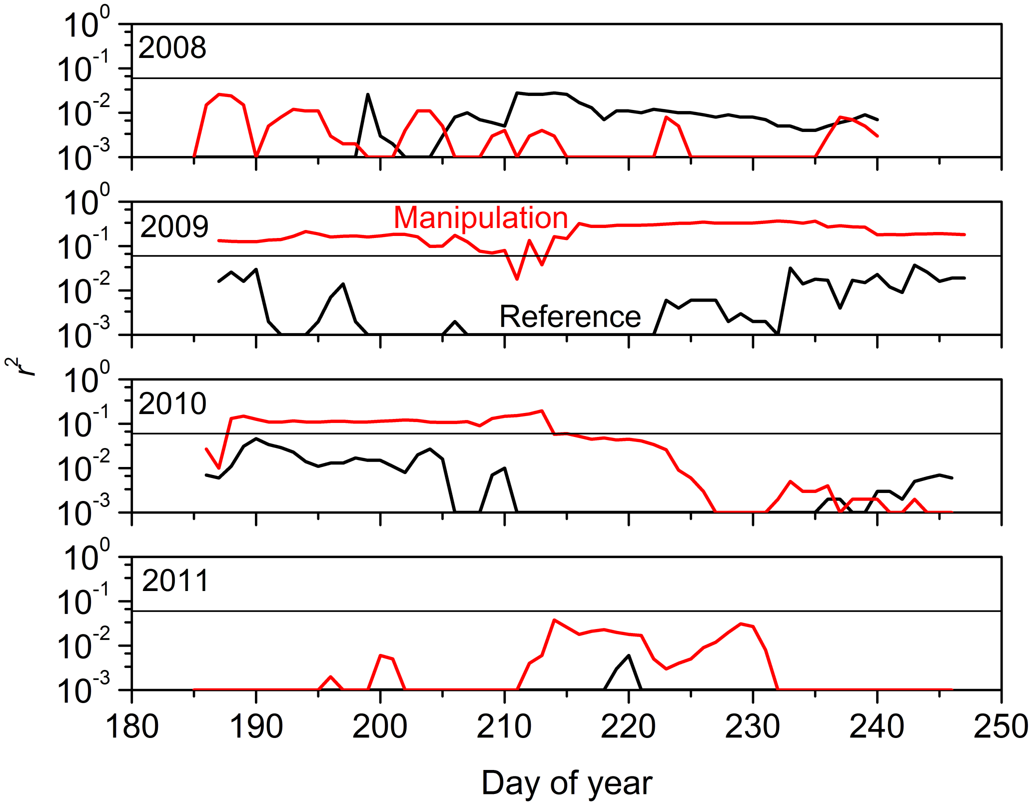

Figure 2. Rolling window (window width = 50 days) conditional heteroskedasticity tests for chlorophyll-*a* time series from the manipulated Peter Lake (red) and the reference Paul Lake (black). The black horizontal line represents the critical value for the conditional heteroskedasticity test. Values above the horizontal line indicate significant ($p < 0.1$) conditional heteroskedasticity. Values below the horizontal line indicate non-significant ($p > 0.1$) conditional heteroskedasticity. For display on the $\log_{10}$-scale, values < 0.001 have been plotted as 0.001.

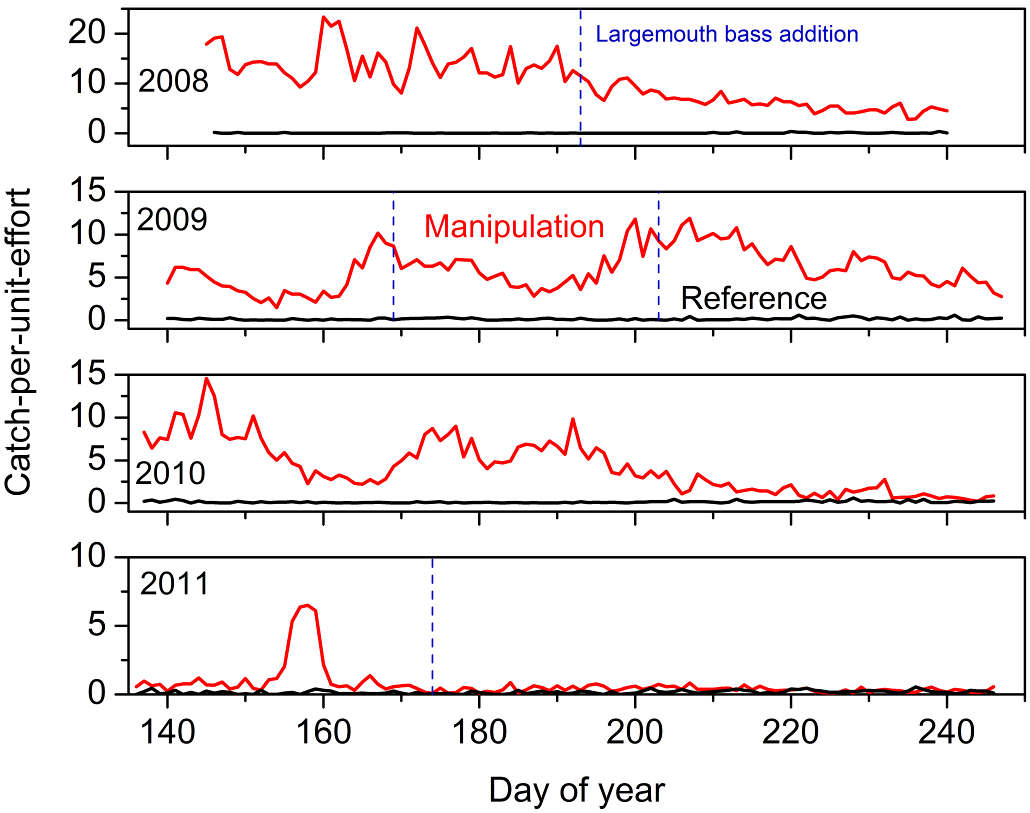

Figure 3. Daily minnow trap catches (catch trap^{-1} day^{-1}) from the littoral zone of the manipulated Peter Lake (red) and reference Paul Lake (black) systems. Vertical dashed blue lines denote the timing of largemouth bass additions to the manipulated Peter Lake. Note the vertical axis scales are different between years for display purposes.

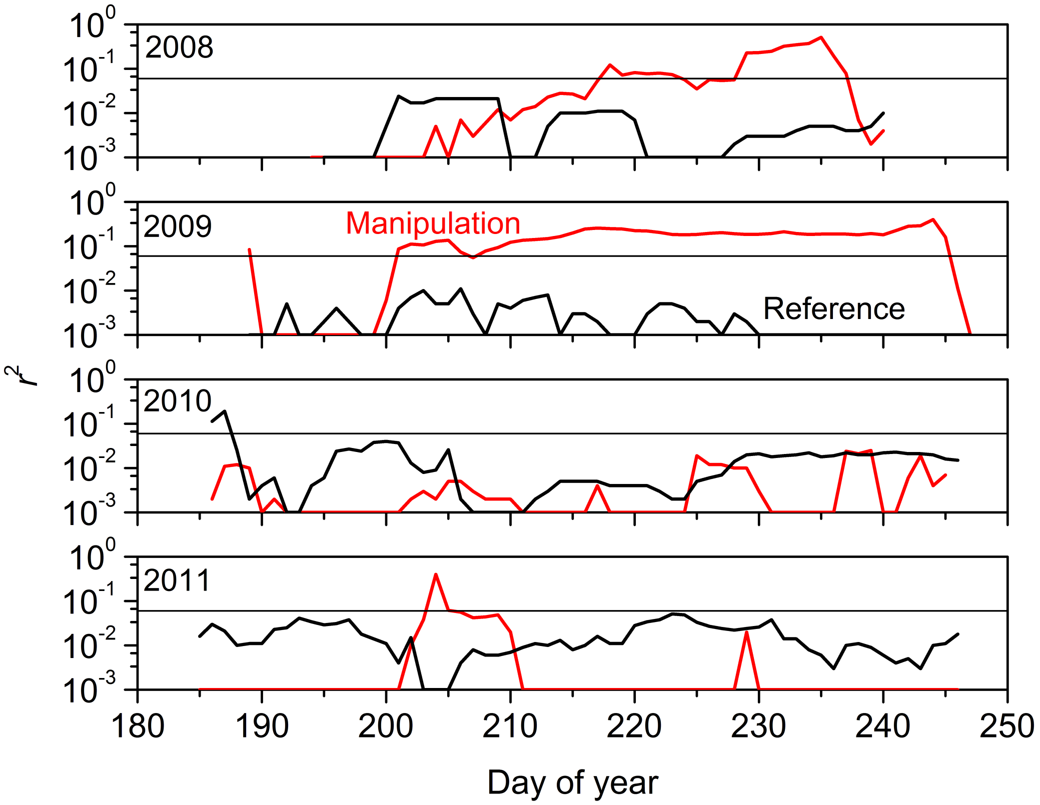

Figure 4. Rolling window (window width = 50 days) conditional heteroskedasticity tests for minnow trap catches (catch trap^{-1} day^{-1}) the manipulated Peter Lake (red) and the reference Paul Lake (black). The black horizontal line represents the critical value for the conditional heteroskedasticity test. Values above the horizontal line indicate significant ($p < 0.1$) conditional heteroskedasticity. Values below the horizontal line indicate non-significant ($p > 0.1$) conditional heteroskedasticity. For display on the $\log_{10}$-scale, values < 0.001 have been plotted as 0.001.

CHAPTER 6: SUMMARY AND CONCLUSIONS

This dissertation shows that tests for conditional heteroskedasticity are a powerful leading indicator of ecosystem regime shifts that also minimize false positive warnings. Chapters two and three show that conditional heteroskedasticity is a general indicator – effective in time in space in response to a variety of regime shift mechanisms. Chapters four and five use data from a whole-ecosystem regime shift experiment to show that conditional heteroskedasticity is an effective indicator at spatial and temporal scales relevant to ecosystem management. Moving window autocorrelation and variance analyses from the ecosystem experiment vary in ways that make results difficult to interpret without detailed understanding of ecosystem properties. Conditional heteroskedasticity is more practical than autocorrelation and variance because conditional heteroskedasticity has a built in threshold that aids in interpretation. Hence, the overall contribution of this dissertation is that it advances early warning analysis by proving the efficacy of a powerful, but easy to interpret early warning indicator.

A variety of early warning indicators for regime shifts exist, but few have been tested with data from real ecosystems (e.g. Carpenter et al. 2011; Dakos et al. 2012; Seekell et al. 2012). To date, the lake experiment detailed in Chapter 5 is the only ecosystem-scale test of early warning indicators. A critical research need is further tests at spatial and temporal scales relevant to ecosystem management. For instance, a variety of studies provide proof-of-concept for early warning indicators in biological systems (e.g. Drake and Griffen 2010), but no analysis based on field or laboratory data exists that shows that early warnings come in time to avert an unwanted shift through adaptive management. If early warning indicators do come in time, synthesis work may be necessary to determine if governance structures can maintain monitoring programs for the required time or if governance structures can respond in enough time to avert a transition. In the end, logistical challenges associated with environmental monitoring and the ability of managers to respond to early warning indicators could be limiting steps that are more challenging then the derivation and application of early warning indicators.

Early warning dynamics may also be interpreted as indirect metrics to test the form (e.g. linear or non-linear) of ecosystem dynamics. For instance, variance and autocorrelation only increase together prior to a regime shift. If these indicators increase in data prior to a historic shift, the shift was likely due to nonlinear dynamics. If the indicators do not exist, the shift was likely due to linear dynamics. These types of indirect indicators may be advantageous for testing hypotheses in ecological data, which typically are not abundant enough to apply direct tests for nonlinearity (see Chapter 4). Climatologists have now used early warning indicators for this purpose (e.g. Lenton et al. 2012), but there have not yet been applications to ecological data. This is an exciting new potential for early warning indicators.

Little is known about the prevalence of conditional heteroskedasticity in ecosystem time series (Chapter 2). The model analyses and whole-ecosystem experiment in this dissertation suggest that conditional heteroskedasticity exists in unstable ecosystems, but not in stable ecosystems. However, it is not yet clear if conditional heteroskedasticity exists naturally in physical or biological characteristics of ecosystems not included in this dissertation and, if yes, what causes conditional heteroskedasticity. Conditional heteroskedasticity is pervasive in other disciplines (e.g. economics) and if uncovered in ecological time series, tests for the origin of conditional heteroskedasticity could unveil unique ecosystem dynamics and new understanding of controls on patterns in ecosystem time series (e.g. Lamoureux and Lastrapes 1990). Such analyses would be novel contributions to the ecological literature and a direct extension of this dissertation. The availability of long-term datasets through the Long-term Ecological Research Network and data repositories like The Knowledge Network for Biocomplexity stand to facilitate widespread evaluation of conditional heteroskedasticity in a variety of ecosystems.

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Appendix 1: Worked examples of test for conditional heteroskedasticity

This appendix to Chapter 2 contains worked examples of a test for conditional heteroskedasticity.

Example 1: Short time series with no conditional heteroskedasticity

We arbitrarily selected a subset of twenty sequential points from the discrete *E. coli* time series without regime shift. The full time series is displayed in Figure A1.1A. The vertical blue lines mark the beginning and end of the subset. Figure A1.1B displays the subset.

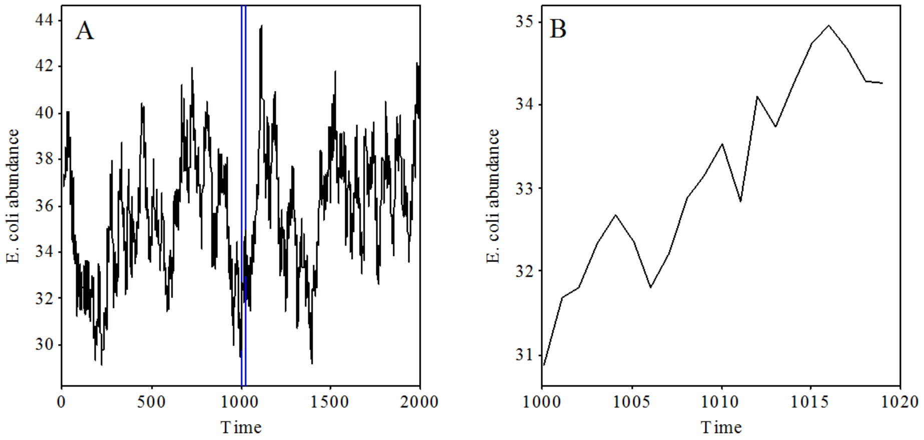

Fig. A1.1. A) *E. coli* dynamics model without regime shift. The vertical blue lines mark the subset of data used in this example. B) Time series of the subset of data from panel A used in this example.

The 20 values from the subset are in the first row of the below table.

Data	30.86	31.67	31.79	32.33	32.67	32.35	31.80	32.20	32.87	33.16	33.54	32.84	34.11	33.74	34.27	34.75	34.96	34.68	34.28	34.26

Step 1: Lag the data one time step. The lagged data are in a second row (highlighted in yellow). Fit an AR(1) model using ordinary least squares regression. The AR model is $Y_t = a + \rho Y_{t\text{-}1} + e$, where Y_t is the measurement at time t, a is a constant, ρ is the autoregressive parameter, $Y_{t\text{-}1}$ is the previous measurement, and e is an error term. The residuals from the AR(1) model are in a third row (highlighted in green).

Data	30.86	31.67	31.79	32.33	32.67	32.35	31.80	32.20	32.87	33.16	33.54	32.84	34.11	33.74	34.27	34.75	34.96	34.68	34.28	34.26
Lagged data		30.86	31.67	31.79	32.33	32.67	32.35	31.80	32.20	32.87	33.16	33.54	32.84	34.11	33.74	34.27	34.75	34.96	34.68	34.28
AR(1) Residuals		0.24	0.30	0.13	0.03	-0.58	-0.86	0.00	0.34	0.07	0.22	-0.80	1.04	-0.37	0.46	0.51	0.32	-0.14	-0.30	0.01

Step 2: Square the AR(1) residuals. The squared residuals are added to a new row in the table and are highlighted in yellow.

Data	30.86	31.67	31.79	32.33	32.67	32.35	31.80	32.20	32.87	33.16	33.54	32.84	34.11	33.74	34.27	34.75	34.96	34.68	34.28	34.26
Lagged data		30.86	31.67	31.79	32.33	32.67	32.35	31.80	32.20	32.87	33.16	33.54	32.84	34.11	33.74	34.27	34.75	34.96	34.68	34.28
AR(1) residuals		0.24	0.30	0.13	0.03	-0.58	-0.86	0.00	0.34	0.07	0.22	-0.80	1.04	-0.37	0.46	0.51	0.32	-0.14	-0.30	0.01
Squared residuals		0.06	0.09	0.02	0.00	0.34	0.74	0.00	0.11	0.00	0.05	0.64	1.08	0.13	0.21	0.26	0.10	0.02	0.09	0.00

Step 3: Lag the squared residuals from step 2. The lagged, squared residuals are added to a new row in the table and highlighted in yellow.

Data	30.86	31.67	31.79	32.33	32.67	32.35	31.80	32.20	32.87	33.16	33.54	32.84	34.11	33.74	34.27	34.75	34.96	34.68	34.28	34.26
Lagged data		30.86	31.67	31.79	32.33	32.67	32.35	31.80	32.20	32.87	33.16	33.54	32.84	34.11	33.74	34.27	34.75	34.96	34.68	34.28

AR(1) residuals		0.24	0.30	0.13	0.03	-0.58	-0.86	0.00	0.34	0.07	0.22	-0.80	1.04	-0.37	0.46	0.51	0.32	-0.14	-0.30	0.01
Squared residuals		0.06	0.09	0.02	0.00	0.34	0.74	0.00	0.11	0.00	0.05	0.64	1.08	0.13	0.21	0.26	0.10	0.02	0.09	0.00
Lagged squared residuals			0.06	0.09	0.02	0.00	0.34	0.74	0.00	0.11	0.00	0.05	0.64	1.08	0.13	0.21	0.26	0.10	0.02	0.09

Step 4: Fit an ordinary least squares regression where the squared residuals from Step 2 are the dependent variable and the lag of the squared residuals from step 3 are the independent variable. The regression results are below.

Predictor	Coefficient	Std. Error Coefficient	*T*	*p*
Constant	0.16132	0.08932	1.81	0.090
Lagged squared Residuals	0.2497	0.2439	1.02	0.321

$r^2 = 0.061$	$n = 18$

Step 5: The Lagrange Multiplier test statistic for heteroskedasticity is the product of the r^2 value highlighted in green in the above regression results table and the sample size in step 4 highlighted in light blue in the above table (0.061*18 = 1.098).

Step 6: Evaluate the probability of finding the Lagrange Multiplier test statistic if there is no conditional heteroskedasticity by comparing the test statistic to a chi-square distribution with one degree of freedom. The observed test statistic (LM = 1.098) is likely given that there is no conditional heteroskedasticity ($p = 0.22$) so we conclude there is not conditional heteroskedasticity in this time series.

Example 2: Short time series with conditional heteroskedasticity

We arbitrarily selected a subset of fifteen sequential points from the planktivore biomass time series with regime shift from the continuous lake food-web model. The full time series is displayed in Figure A1.2A. The vertical blue lines mark the beginning and end of the subset and the vertical red line marks the critical transition point. Figure A1.2B displays the subset.

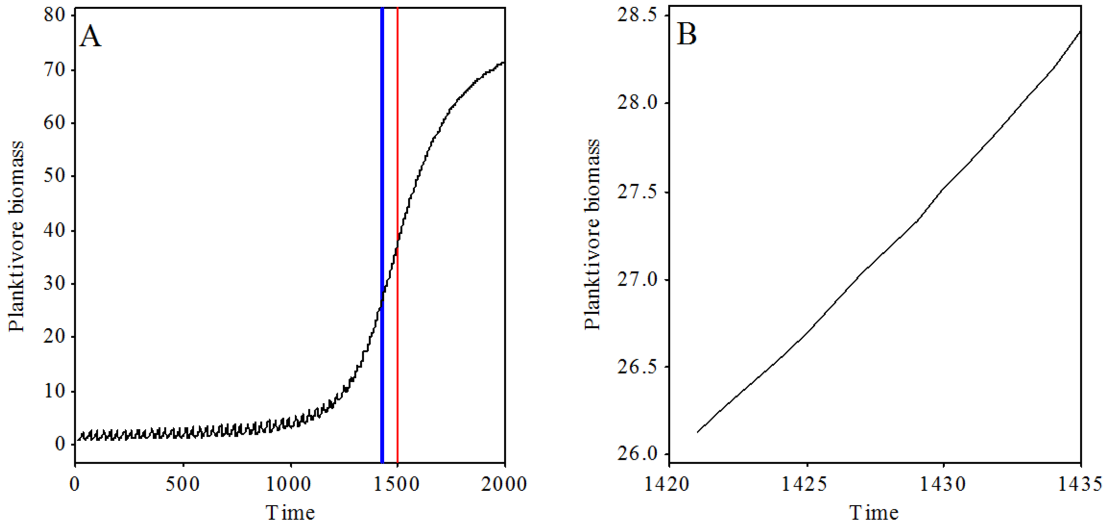

Fig. A1.2. A) Planktivore biomass time series from the continuous lake food-web model with regime shift. The vertical blue lines mark the beginning and end of the data subset. The vertical red line marks the critical transition point. B) The subset of fifteen points from the planktivore biomass time series with regime shift.

The 15 values from the subset are in the first row of the below table.

Data	26.13	26.27	26.41	26.55	26.70	26.86	27.03	27.18	27.33	27.51	27.68	27.85	28.03	28.20	28.42

Step 1: Lag the data one time step. The lagged data are in a second row (highlighted in yellow). Fit an AR(1) model using ordinary least squares regression. The residuals from the AR(1) model are in the third row (highlighted in green).

Data	26.13	26.27	26.41	26.55	26.70	26.86	27.03	27.18	27.33	27.51	27.68	27.85	28.03	28.20	28.42
Lagged data		26.13	26.27	26.41	26.55	26.70	26.86	27.03	27.18	27.33	27.51	27.68	27.85	28.03	28.20
AR(1) Residuals		0.002	-0.002	-0.005	0.003	0.010	0.010	-0.010	-0.016	0.016	-0.009	0.001	-0.009	-0.019	0.27

Step 2: Square the residuals from the AR(1) residuals. The squared residuals are highlighted in yellow in the fourth row of the table. We plotted the squared residuals in Figure A1.3 because the values are very small and the variability is difficult to appreciate in Fig S2B.

Data	26.13	26.27	26.41	26.55	26.70	26.86	27.03	27.18	27.33	27.51	27.68	27.85	28.03	28.20	28.42
Lagged data		26.13	26.27	26.41	26.55	26.70	26.86	27.03	27.18	27.33	27.51	27.68	27.85	28.03	28.20
AR(1) residuals		0.002	-0.002	-0.005	0.003	0.010	0.010	-0.010	-0.016	0.016	-0.009	0.001	-0.009	-0.019	0.27
Squared residuals		0.0000	0.0000	0.0000	0.0000	0.0001	0.0001	0.0001	0.0003	0.0003	0.0001	0.0000	0.0001	0.0003	0.0007

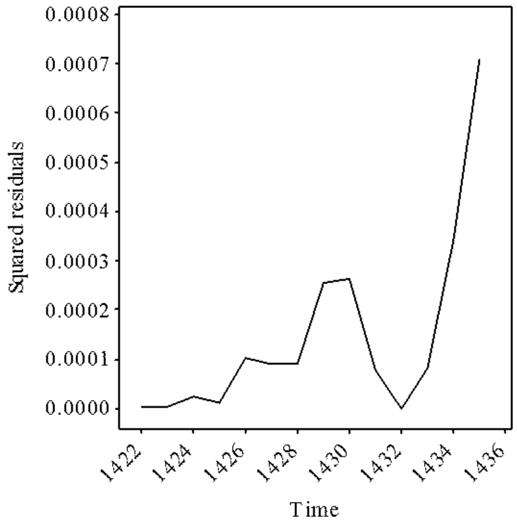

Fig. A1.3. Squared residuals by time step from the continuous lake food-web model subset. The variance increases with time.

Step 3: Lag the squared residuals from step 2. The lagged, squared residuals are added to the fifth row in the table and are highlighted in yellow.

Data	26.13	26.27	26.41	26.55	26.70	26.86	27.03	27.18	27.33	27.51	27.68	27.85	28.03	28.20	28.42
Lagged data		26.13	26.27	26.41	26.55	26.70	26.86	27.03	27.18	27.33	27.51	27.68	27.85	28.03	28.20
AR(1) residuals		0.002	-0.002	-0.005	0.003	0.010	0.010	-0.010	-0.016	0.016	-0.009	0.001	-0.009	-0.019	0.27
Squared residuals		0.0000	0.0000	0.0000	0.0000	0.0001	0.0001	0.0001	0.0003	0.0003	0.0001	0.0000	0.0001	0.0003	0.0007
Lagged squared residuals			0.0000	0.0000	0.0000	0.0000	0.0001	0.0001	0.0001	0.0003	0.0003	0.0001	0.0000	0.0001	0.0003

Step 4: Fit an ordinary least squares regression where the squared residuals from Step 2 are the dependent variable and the lag of the squared residuals from step 3 are the independent variable. The regression results are below.

Predictor	Coefficient	Std. Error Coefficient	*T*	*p*
Constant	0.00003042	0.000005660	0.54	0.602
Lagged squared Residuals	1.2291	0.3753	3.27	0.007

$r^2 = 0.494$	$n = 13$

Step 5: The Lagrange Multiplier test statistic for heteroskedasticity is the product of the r^2 value highlighted in green in the above regression results table and the sample size highlighted in light blue in the above regression results table (0.494*13 = 6.422).

Step 6: Evaluate the probability of finding the Lagrange Multiplier test statistic if there is no conditional heteroskedasticity by comparing the test statistic to a chi-square distribution with one degree of freedom. This test statistic (LM = 6.422) is unlikely given that there is no conditional heteroskedasticity ($p = 0.006$) so we conclude there is conditional heteroskedasticity in this time series.

Appendix 2: GARCH Model Selection

This appendix to Chapter 4 contains additional results for GARCH model selection.

<u>Model Selection Results</u>

We fit six GARCH(1,1) time series models to filter linear relationships out of the fish catch time series. First, autoregressive models with one ($y_t = b_1 y_{t-1}$) to six lags ($y_t = b_1 y_{t-1} + b_2 y_{t-2} + b_3 y_{t-3} + b_4 y_{t-4} + b_5 y_{t-5} + b_6 y_{t-6}$) were fit to the time series using maximum likelihood. This portion of the model (the structural portion) predicts the mean. Each model also contained four binary dummy variables to adjust for potential shifts in mean between years (i.e. values for the dummy variable for year 200x are 1 if the data are from 200x and 0 otherwise, values for the dummy variable for year 200y are 1 if the data are from 200y and 0 otherwise, and so on). A GARCH(1,1) equation was fit to the residuals of each autoregressive model. A GARCH(1,1) equation is essentially a autoregressive moving average time series model applied to the squared residuals of the structural model. The squared residual is an estimate of error variance at a given time step. Hence the GARCH model seeks to predict error variance based on previous error variances.

The best autoregressive model was then selected on the dual criteria of elimination of autocorrelation from residuals of the structural portion of the model (according to Durbin's *h* test) and minimization of the AICc. A model with three lags was selected as the best fitting structural model because it eliminated autocorrelation ($p = 0.1568$) and minimized the AICc (Table A2.1). For the GARCH portion of the model we used one autoregressive term and one moving average term in each model. We experimented with higher order terms but these did not improve fit. We fit the GARCH models using SAS/ETS version 9.2. The equation for the best fitting GARCH model is:

$$(1)\ y_t = b_1 y_{t-1} + b_2 y_{t-2} + b_3 y_{t-3} +$$

$$b_4 d_{2008} + b_5 d_{2009} + b_6 d_{2010} + b_7 d_{2011} + \varepsilon_t, \quad \varepsilon_t = \sqrt{h_t} z_t$$

$$h_t = a_0 + a_1 \varepsilon_{t-1}^2 + a_2 h_{t-1}$$

where y_t is the state variable, b_1, b_2, b_3 are autoregressive coefficients for the mean, a_k are autoregressive coefficients for the conditional error variance ($\sqrt{h_t}$), b_4, b_5, b_6 are coefficients for the dummy variables d_{2008}, d_{2009}, d_{2010}, d_{2011}.

The three autoregressive lags were significant (Table A2.2). The dummy variables were not significant, but the fitted coefficients were negative which is consistent with a general decline in minnow abundance. The GARCH parameters (a_k) were greater than zero and summed to less than one indicating at good model fit (Engle 2001).

We calculated the BDS test using the “tseries” package in R. The phase plots were created in Origin Pro graphing software.

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Table A2.1. Model comparison statistics for Peter Lake fish time series. The diagnostics statistics are the coefficient of determination (r^2), information criterion (AICc), Durbin's *h* statistic for residual autocorrelation (probability values in parentheses), and Engle's (1982) Lagrange multiplier test for conditional heteroskedasticity (probability values in parentheses). The *h* and LM statistics derive from the structural portion of the model while the r^2 and AICc statistics derive from the full GARCH model. The AR-3 model (in bold) was selected because the structural portion of the model eliminated autocorrelation and the AICc values were lower than the other candidate models.

Model	AR r^2	AR AICc	*H*	LM	GARCH r^2	GARCH AICc
AR-1	0.1204	489.040111	-4.8080 (p = 0.0001)	47.6871 (p < 0.0001)	0.1187	323.962301
AR-2	0.1611	470.92655	-3.3225 (p = 0.0004)	82.7283 (p < 0.0001)	0.1579	310.025402
AR-3	**0.1692**	**468.025051**	**-1.0089 (p = 0.1568)**	**83.8402 (p < 0.0001)**	**0.1652**	**305.962521**
AR-4	0.1716	468.785545	-1.2004 (p = 0.1153)	83.0649 (p < 0.0001)	0.1680	307.36322
AR-5	0.1737	469.629508	-1.1461 (p = 0.1262)	88.9607 (p < 0.0001)	0.1696	309.392506
AR-6	0.1758	470.597107	-2.9288 (p = 0.0018)	93.2569 (p < 0.0001)	0.1711	310.998679

Table A2.2. Statistical results for the best fitting GARCH model (three autoregressive lags).

Variable (term in equation1)	Coefficient	Standard error	*t*-value	Probability value
AR-Lag1 (b_1)	-0.3909	0.0510	-7.66	<0.0001
AR-Lag2 (b_2)	-0.2580	0.0588	-4.39	<0.0001
AR-Lag3 (b_3)	-0.1255	0.0568	-2.21	0.0271
2008 dummy (b_4)	-0.0340	0.0240	-1.41	0.1574
2009 dummy (b_5)	-0.0109	0.0245	-0.45	0.6558
2010 dummy (b_6)	-0.0187	0.0278	-0.67	0.5005
2011 dummy (b_7)	-0.0101	0.0407	-0.25	0.8041
ARCH intercept (a_0)	0.004116	0.001844	2.23	0.0256
ARCH parameter (a_1)	0.1821	0.0429	4.25	<0.0001
GARCH parameter (a_2)	0.7995	0.0421	18.98	<0.0001

Appendix 3: Additional Results for Empirical Tests of Conditional Heteroskedasticity as an Early Warning Indicator

This appendix to Chapter 5 contains additional empirical results including moving window tests for autocorrelation and variance and a sensitivity analysis.

Moving window autocorrelation and coefficient of variation

We calculated moving window lag-1 autocorrelation coefficients and coefficients of variation (standard deviation / mean) for the phytoplankton and minnow trap time series. The purpose of these plots is to provide a means for comparison between the behavior of these two more widely applied indicators and conditional heteroskedasticity. The first three years of autocorrelation and coefficient of variation for the phytoplankton time series were previously described by Carpenter and others (2011). We use 28 day moving windows to remain consistent with their analysis.

Autocorrelation was near one in the manipulation system prior to the shift in 2009 and 2010, a strong indication of an impending regime shift (Carpenter and others 2011) (Figure A3.1 red lines). However, autocorrelation in the manipulation system also approached one at the end of 2011 when the system had stabilized at a new state (Figure A3.1). Autocorrelation was highly variable in the reference system and autocorrelation had increasing trends for substantial portions of 2008 and 2011 (Figure A3.1, black lines).

Variance was high and increasing in the manipulation lake in 2009 and remained high in 2010, indicative of an impending regime shift (Figure A3.1, red lines). Variance was lower in 2011 and decreasing, consistent with a system that had stabilized at a new state. Variance was high in the reference lake in 2008, but this was largely a function of a single high chlorophyll-a measurement on day of year 153. (Figure A3.1 black lines, Figure 1 in the main text). Variance was generally low in the reference lake, but had an increasing trend in 2009 even though the system was stable.

Autocorrelation was increasing in the manipulation lake minnow trap time series in 2008 and remained near one until 2011 when the system stabilized at the new state (Figure A3.2 red lines). This pattern is indicative of an impending regime shift. Autocorrelation was highly variable in the reference system, but did not approach one indicating no impending shift (Figure A3.2 black lines).

The coefficient of variation was low and stable for the fish catch time series in the manipulation lake (Figure A3.2 red lines). This is not consistent with early warning of an impending regime shift. The coefficient of variation in the reference system was generally low and stable (Figure A3.2 black lines). In 2008 the coefficient of variation was high but not trending in the reference system. These patterns in the reference system are consistent with a system not approaching a regime shift.

Autocorrelation and variance statistics in this analysis provide early warning of the experimental regime shift in the manipulation lake (Carpenter and others 2011). However, these statistics are highly variable in the reference system and there are extended periods with increasing autocorrelation and variance even though the system is stable. While such trends may happen due to chance, there is a tendency to apply meaning to them (cf. Tversky and Kahneman 1971) especially in short time series that will likely be typical of many applications of early warning indicators (e.g., Carpenter and others 2011, Bestelmeyer and others 2011). For instance, variance was increasing throughout 2009 in the reference system chlorophyll-a time series. Without additional years of data for context, a manager might conclude that there is early warning of a regime shift due to rising variance. The principal advantage of conditional heteroskedasticity testing is that probability values aid in discerning when early warnings are meaningful. Much like autocorrelation and variance, moving window conditional heteroskedasticity test statistics are highly variable (Figure A3.2). However, the threshold level for significance provides an easy to interpret benchmark on whether or not the indicator is possibly meaningful. In the case of the 2009 reference system chlorophyll-*a* time series, there was no significant conditional heteroskedasticity tests indicating that even though there may be trends within sub-sets of the moving window results, these due not represent meaningful early warnings.

Figure A3.1. Moving window (28 day) lag-1 autocorrelation coefficient and coefficient of variation (standard deviation / mean) for phytoplankton time series in the reference (black) and manipulation (red) system. Increasing autocorrelation and autocorrelation near one are consistent with early warning of regime shift. Increasing variation is consistent with early warning of a regime shift.

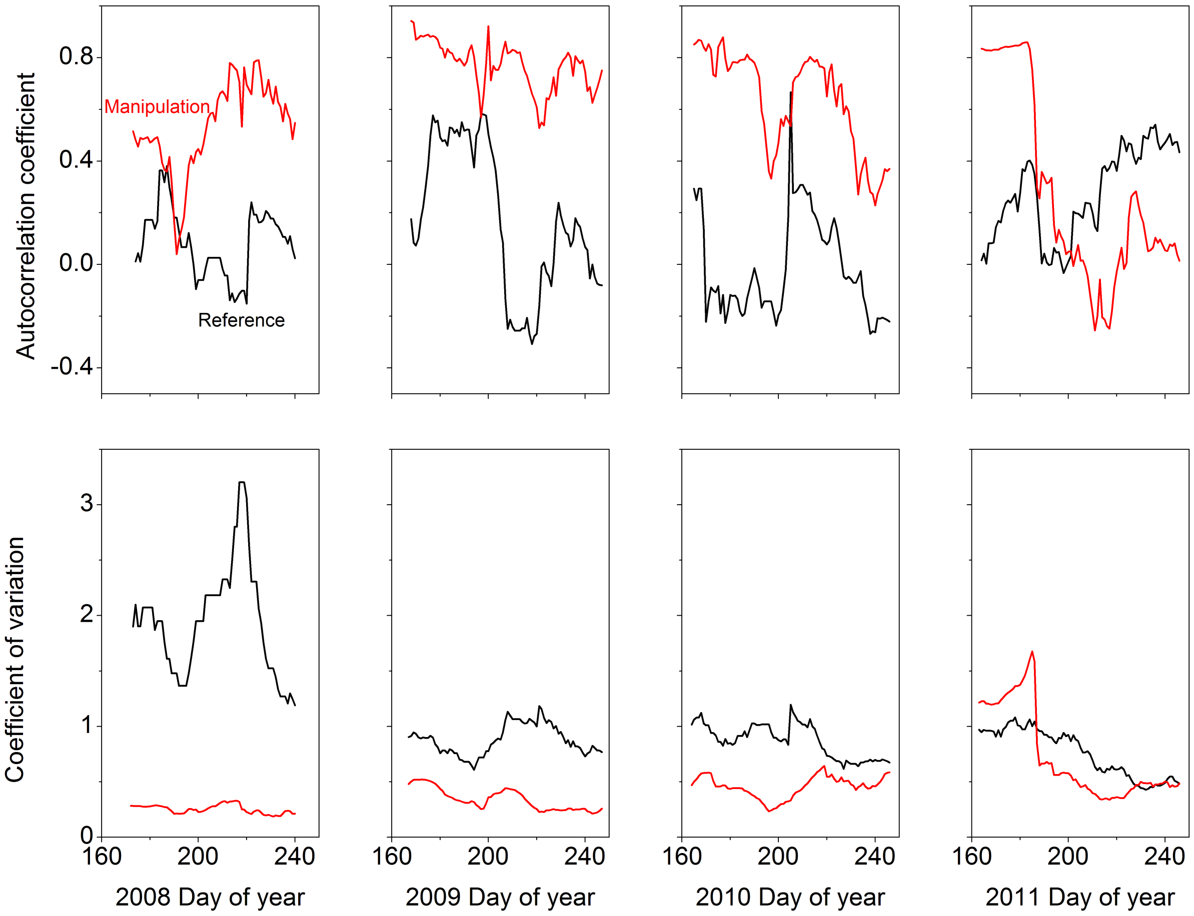

Figure A3.2. Moving window (28 day) lag-1 autocorrelation coefficient and coefficient of variation (standard deviation / mean) for mean minnow trap time series in the reference (black) and manipulation (red) system. Increasing autocorrelation and autocorrelation near one are consistent with early warning of regime shift. Increasing variation is consistent with early warning of a regime shift.

Sensitivity of conditional heteroskedasticity testing to window size selection

We applied conditional heteroskedasticity tests using variably sized moving windows (widths = 30, 40, 60, 70 days). The outcome of this analysis is 16 figures each for fish and chlorophyll-a time series (4 years × 4 window widths). The four window widths for each year are arranged vertically. If the general pattern of significant vs. non-significant tests is consistent vertically, the conditional heteroskedasticity test is robust to window size selection. Wider window widths have more power to detect conditional heteroskedasticity (cf. Engle and others 1985). However, larger window widths reduce the total number of windows, which obscures delimiting the location of the shift and requires that longer time series be collected before application of indicators can begin. Hence the windows begin later in the year for longer window widths because more data is necessary before application can begin.

Conditional heteroskedasticity tests were robust to window size selection for phytoplankton time series (Figure A3.3). There was no significant conditional heteroskedasticity in 2008 or 2011 regardless of window width. There was significant conditional heteroskedasticity for extended periods of time in the manipulated lake in 2009 and 2010, but not in the reference lake. Conditional heteroskedasticity tests were relatively robust to window size selection for the fish catch per unit effort time series (Figure A3.4). This broke down for narrow windows though (n = 30). Wider windows provided consistent results.

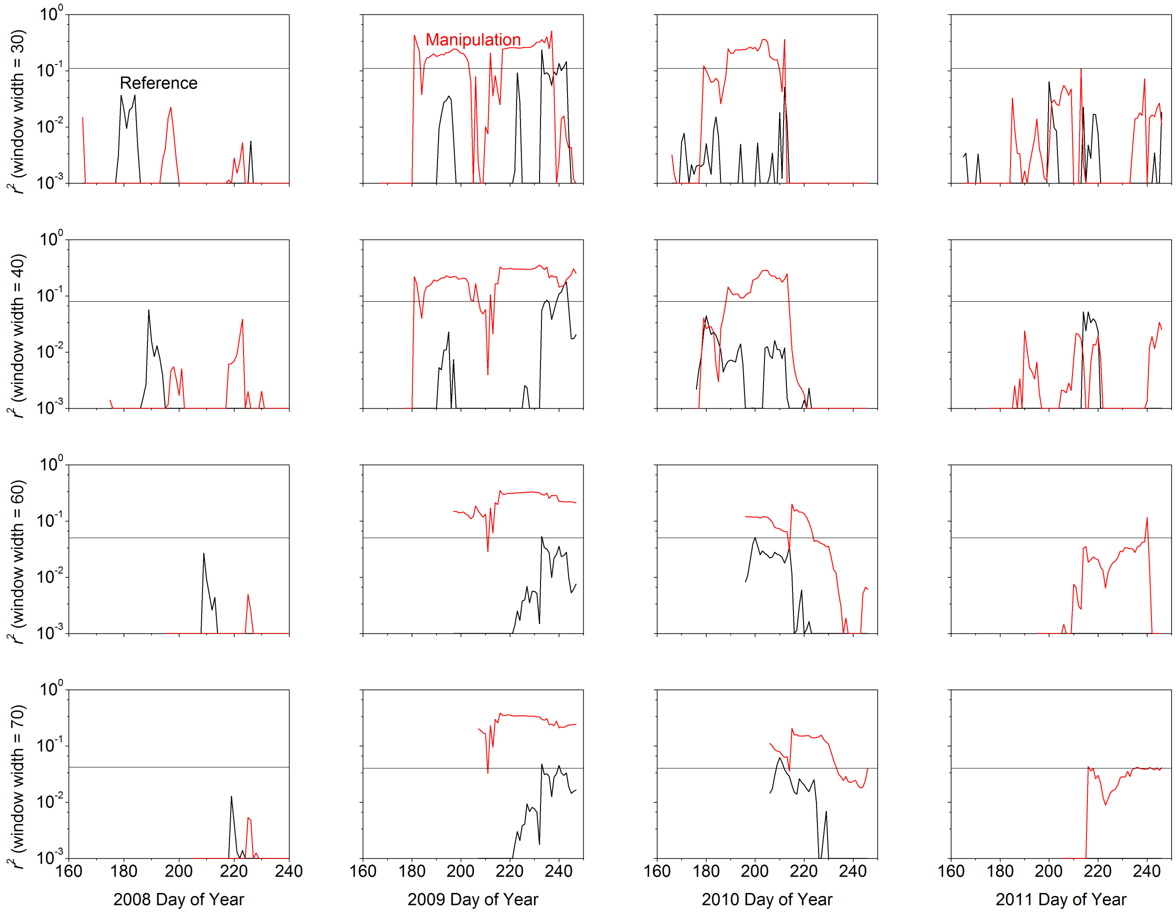

Figure A3.3: Conditional heteroskedasticity tests on phytoplankton time series using variably size moving windows (n = 30, 40, 60, 70). Columns separate years and rows separate window widths. Red lines denote the manipulated Peter Lake. Black lines denote the reference Paul Lake. The horizontal lines denote the threshold level for significance ($p = 0.1$). Tests above the horizontal lines are significant ($p \leq 0.1$). Tests below the horizontal lines are not significant ($p > 0.1$).

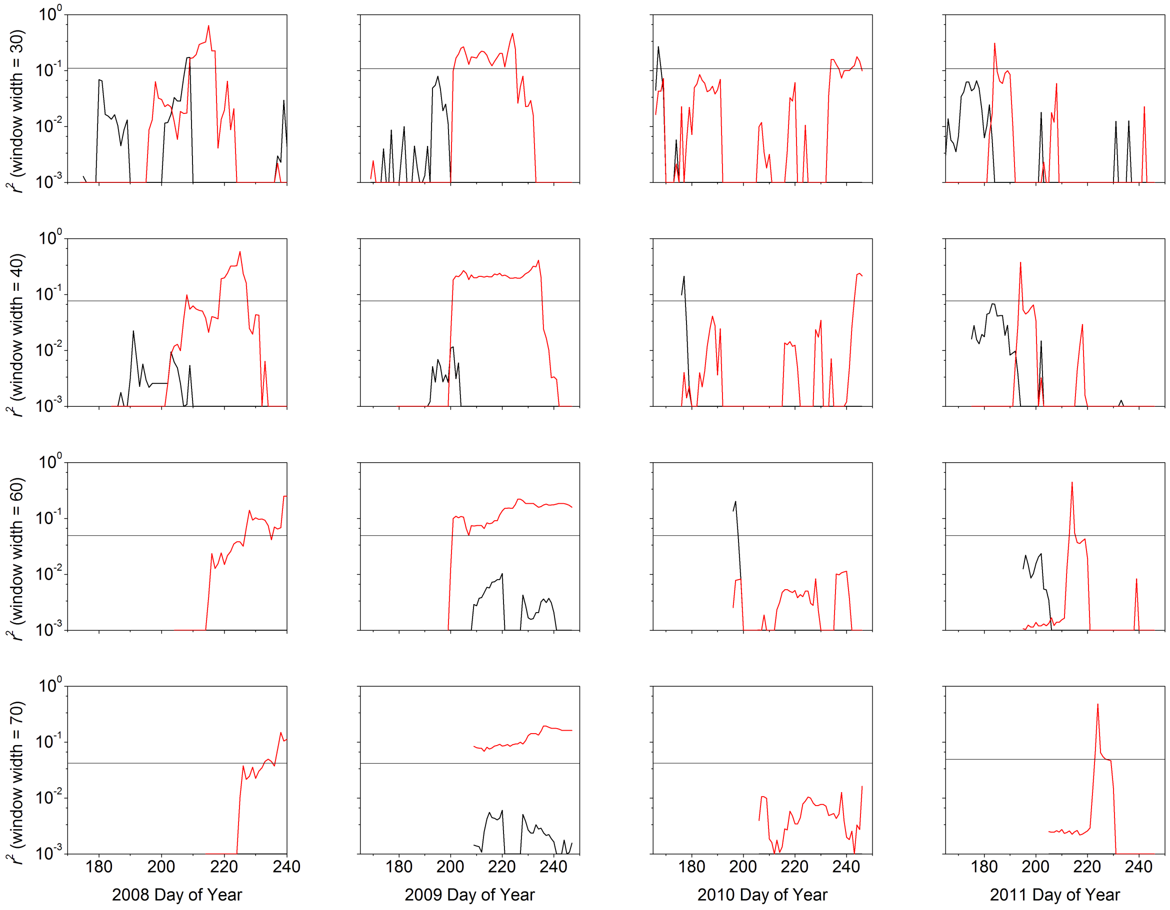

Figure A3.4: Conditional heteroskedasticity tests on minnow trap time series using variably sized moving windows (n = 30, 40, 60, 70). Columns separate years and rows separate window widths. Red lines denote the manipulated Peter Lake. Black lines denote the reference Paul Lake. The horizontal lines denote the threshold level for significance ($p = 0.1$). Tests above the horizontal lines are significant ($p \leq 0.1$). Tests below the horizontal lines are not significant ($p > 0.1$).

Conditional heteroskedasticity test sensitivity to time series filter selection

We applied moving window (window with = 50 days) conditional heteroskedasticity tests using autoregressive time series models with two to six autoregressive lags (lower order lags included). Conditional heteroskedasticity tests are robust to time series model selection if the conditional heteroskedasticity tests for each model follow a similar pattern and are of a similar magnitude when plotted together. For the phytoplankton time series, conditional heteroskedasticity tests were robust to time series model selection except during the beginning of 2010 (Figure A3.5). Here, low order models (AR Lag-2 and AR Lag-3) produce tests statistics that are much greater than the higher order models in the reference system and test statistics that are much lower than the higher order models in the manipulation system. This could lead to false positive early warnings in the reference system and false negatives in the manipulation system. High order models providing similar results is consistent with the idea that over specifying the number of autoregressive lags in the time series model will not cause the conditional heteroskedasticity test to perform more poorly than a correctly specified lower order model (Lumsdaine and Ng 1999). Conditional heteroskedasticity tests appeared robust to time series model selection when applied to the minnow trap time series (Figure A3.6).

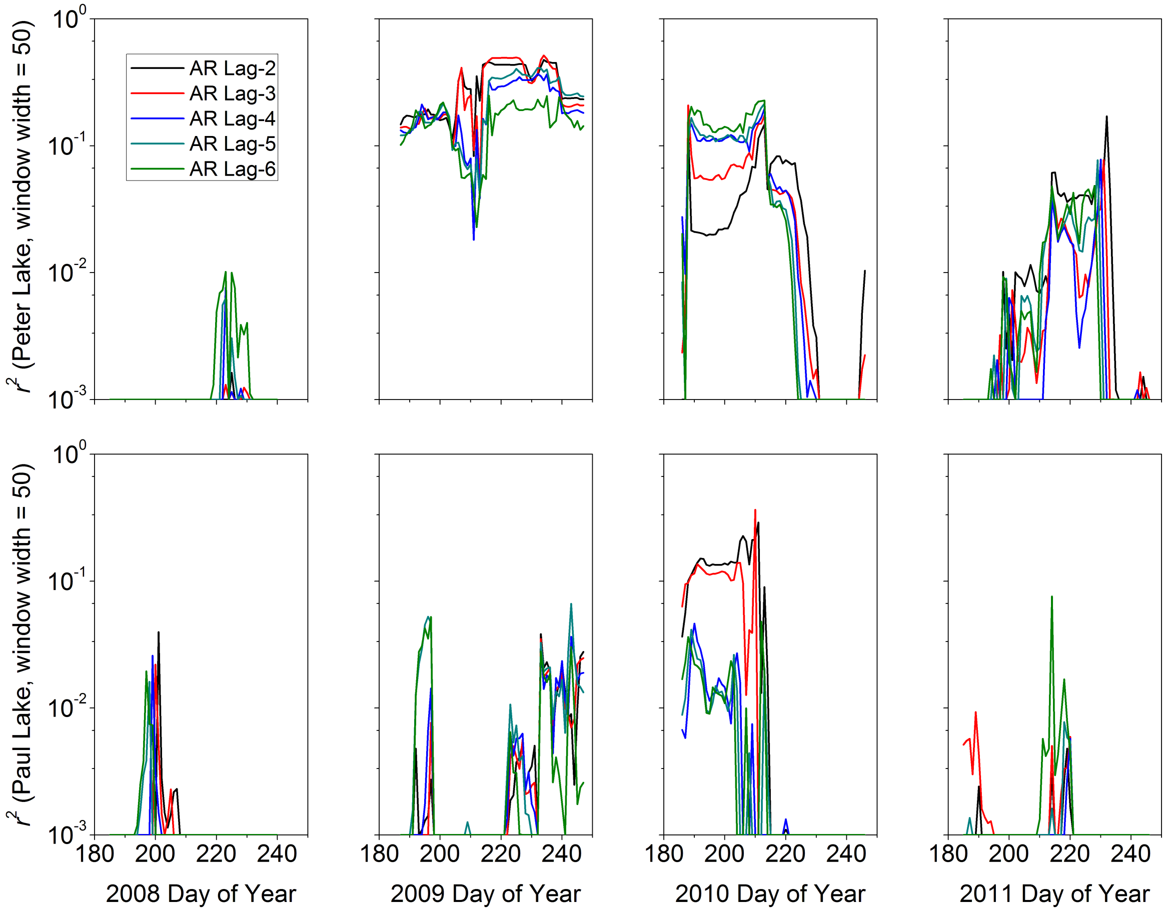

Figure A3.5. Conditional heteroskedasticity test sensitivity to time series model selection when applied to phytoplankton time series. If the differently color lines, representing different autoregressive models (autoregressive lags 2-6, including lower order lags), follow the same pattern, the conditional heteroskedasticity test is robust to time series model selection. If there is considerable space between different time series models, conditional heteroskedasticity testing is not robust to the choice of time series model.

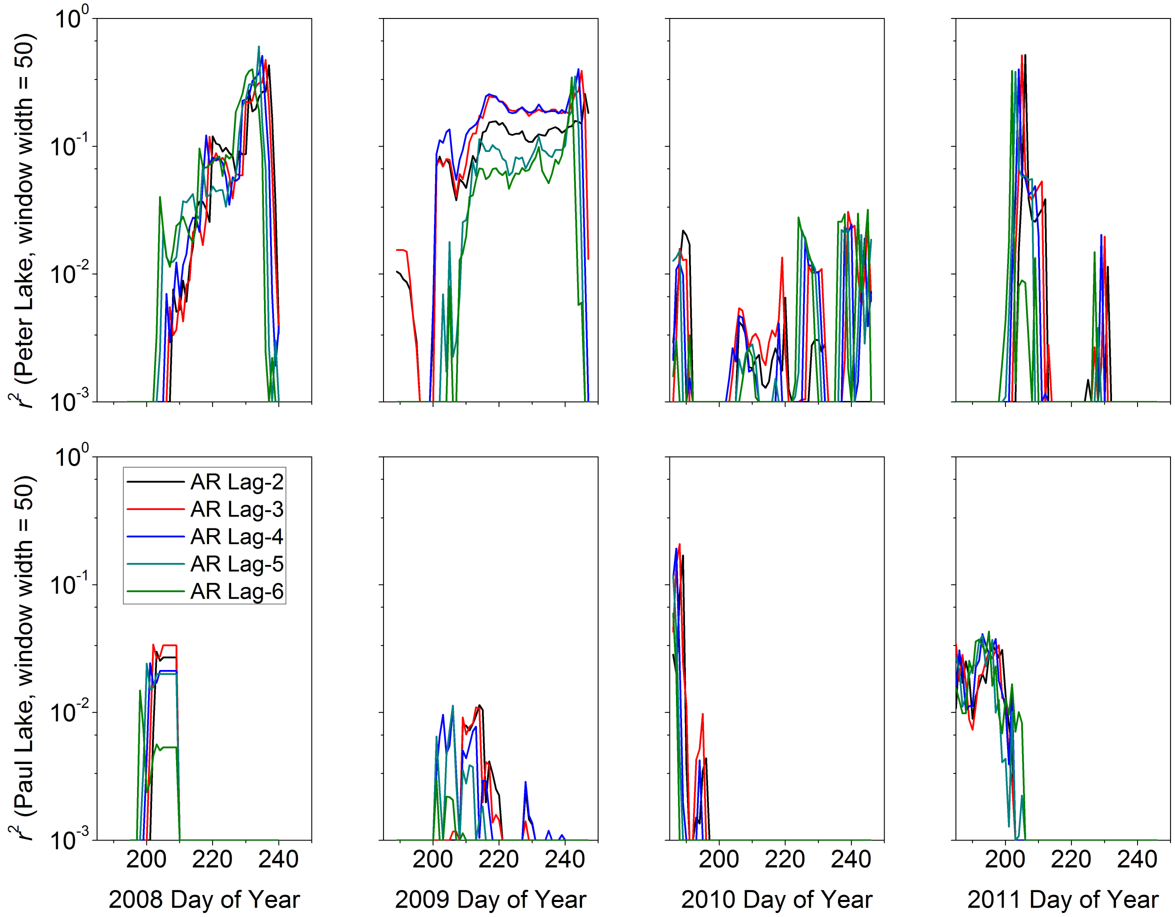

Figure A3.6. Conditional heteroskedasticity test sensitivity to time series model selection when applied to minnow trap time series. If the differently color lines, representing different autoregressive models (autoregressive lags 2–6, including lower order lags), follow the same pattern, the conditional heteroskedasticity test is robust to time series model selection. If there is considerable space between different time series models, conditional heteroskedasticity testing is not robust to the choice of time series model.

Conditional heteroskedasticity test to sensitivity to threshold probability value selection

In the main text we selected a threshold for significance of $p = 0.1$ *a priori* because of the relatively small sample size ($n = 50$) used in each window (cf. Engle et al. 1985). Threshold levels for the significance of probability values are arbitrary for all statistics. In this case higher thresholds increase the power of conditional heteroskedasticity tests. Lower thresholds improve the ability of the indicator to prevent false positive warnings. Hence in field settings the critical threshold may be adjusted based on sample size to increase power or minimize false positives.

We applied moving window conditional heteroskedasticity tests using autoregressive lag-4 models, 50-day windows. We tabulated the number of significant tests in each time series using critical probability values of $p = 0.1$ and $p = 0.05$. Realistically, these critical thresholds are very close to each other (difference = 0.05) so there should be minimal differences in number of significant tests between the thresholds. Higher threshold probabilities will always have the same number or more significant tests than lower threshold probability values. There was almost no difference in number of significant tests (Table A3.1).

Table A3.1. Number of significant conditional heteroskedasticity tests (with Lag-4 autoregressive time series models and 50 day moving windows) at thresholds of *p* = 0.1 and *p* = 0.05 for significance.

Lake	Year	Time series	Number of significant tests		Total number of tests
			P = 0.1	P = 0.05	
Peter	2008	Phytoplankton	0	0	56
Paul	2008	Phytoplankton	0	0	56
Peter	2008	Fish	15	9	47
Paul	2008	Fish	0	0	46
Peter	2009	Phytoplankton	59	56	61
Paul	2009	Phytoplankton	0	0	61
Peter	2009	Fish	44	42	59
Paul	2009	Fish	0	0	59
Peter	2010	Phytoplankton	26	26	61
Paul	2010	Phytoplankton	0	0	61
Peter	2010	Fish	0	0	61
Paul	2010	Fish	2	2	61
Peter	2011	Phytoplankton	1	0	62
Paul	2011	Phytoplankton	0	0	62
Peter	2011	Fish	2	1	62
Paul	2011	Fish	0	0	62

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