Theor Ecol (2013) 6:359–372
DOI 10.1007/s12080-013-0187-3

ORIGINAL PAPER

Regime shifts in a social-ecological system

Steven J. Lade · Alessandro Tavoni · Simon A. Levin · Maja Schlüter

Received: 15 February 2013 / Accepted: 29 April 2013 / Published online: 3 July 2013

Abstract Ecological regime shifts are rarely purely ecological. Not only is the regime shift frequently triggered by human activity, but the responses of relevant actors to ecological dynamics are often crucial to the development and even existence of the regime shift. Here, we show that the dynamics of human behaviour in response to ecological changes can be crucial in determining the overall dynamics of the system. We find a social–ecological regime shift in a model of harvesters of a common-pool resource who avoid over-exploitation of the resource by social ostracism of non-complying harvesters. The regime shift, which can be triggered by several different drivers individually or also in combination, consists of a breakdown of the social norm, sudden collapse of co-operation and an over-exploitation of the resource. We use the approach of generalized modeling to study the robustness of the regime shift to uncertainty over the specific forms of model components such as the ostracism norm and the resource dynamics. Importantly, the regime shift in our model does not occur if the dynamics of harvester behaviour are not included in the model. Finally, we sketch some possible early warning signals for the social–ecological regime shifts we observe in the models.

Keywords Regime shifts · Tipping points · Early warning signals · Bifurcation · Generalized modeling · social–ecological system

S. J. Lade (✉) · M. Schlüter
Stockholm Resilience Centre, Stockholm University,
Kräftriket 2B, 114 19 Stockholm, Sweden
e-mail: steven.lade@stockholmresilience.su.se

S. J. Lade
NORDITA, KTH Royal Institute of Technology,
and Stockholm University, Roslagstullsbacken 23,
106 91 Stockholm, Sweden

A. Tavoni
Grantham Research Institute, London School of Economics,
London, WC2A 2AZ, UK

S. A. Levin
Department of Ecology and Evolutionary Biology,
Princeton University, Princeton, NJ 08544, USA

Introduction

Many ecological systems can undergo large, sudden and long-lasting changes in structure and function (Scheffer et al. 2001). Such changes, often called regime shifts[1] or critical transitions (Scheffer et al. 2009), have been found in a range of ecological systems, including eutrophication of freshwater lakes, soil salinisation, degradation of coral reefs, collapse of fisheries and encroachment of bushland (Biggs et al. 2012a).

Most ecological systems, and especially those systems that are at risk of sudden non-linear changes such as regime shifts, are subject to influence by humans (Millennium Ecosystem Assessment 2005). Furthermore, humans not only influence the ecological system but also adapt their behaviour in response to ecological changes (Folke et al. 2010). However, many traditional ecological modelling approaches reduce the social subsystem to a simple driver, such as fishing pressure or resource extraction rate (Schlüter et al. 2012a). Mirroring this problem in bioeconomic models of the optimal management of renewable

[1] In this article, we use the term 'regime shift' in a social as well as an ecological context. We intend the term 'regime shift' to be understood in such a social context as not (necessarily) a political regime change but rather any recognisably sudden, large and persistent change in the behaviour of relevant actors.

resources, the descriptions of resource dynamics are often very simple, with neither resource nor management strategy capable of regime shifts (with exceptions including recent work from ecological economics such as (Crépin and Lindahl 2009; Horan et al. 2011).

Here, we show that modelling changes in the behaviour of the humans who interact with the ecological system is crucial to understanding regime shifts in the ecological populations. In particular, a central result is that such systems, often referred to as *social–ecological systems* (Berkes and Folke 1998; Carpenter et al. 2009), can display regime shifts that are absent from the ecological subsystem in isolation. We find that even a non-linear linkage between completely linear social and ecological subsystems, which have no regime shifts of their own, can induce regime shifts in the coupled system.

To develop these results, we analyse a social–ecological system that captures essential properties of a class of systems encountered frequently in natural resource management: a common-pool resource where harvesters need to co-operate to restrain their individual extraction to prevent over-harvesting, together with a social mechanism that encourages but does not guarantee such co-operation (Ostrom 1990; 2006). We represent this system using two types of models: a generalized model, where the details of the processes in the system are left unspecified; and simulation models that have functional forms fully specified, as is necessary to perform time series simulations.

We search for possible regime shifts in this social–ecological system by analysing the fold bifurcations of the models. Fold bifurcations, one of a family of precisely mathematically defined qualitative changes in the dynamical behaviour of a system (Kuznetsov 2010), can lead to regime shifts (Scheffer et al. 2001). Bifurcation analysis of the generalized model therefore permits general statements about the presence and robustness of regime shifts over a wide range of systems. This generality is useful when analysing social–ecological systems, in which the specific functional forms required by simulation models can be difficult to determine. Bifurcation analysis of simulation models allows us to test the generalized results in specific cases and to predict the presence and effects of regime shifts with respect to specific parameters of the simulation model.

Since regime shifts are sudden, persistent and often have significant consequences, early warning signals for an impending regime shift would be highly desirable. Early warning signals have recently been developed for regime shifts in ecological and physical systems (Scheffer et al. 2009, 2012). We perform preliminary investigations on the possibility of using these early warnings for regime shifts in social–ecological systems. We use the conventional variance and autocorrelation indicators (Dakos et al. 2012b) as well as the generalized modeling-based early warning signal (Lade and Gross 2012).

Section 'Methods' describes in greater detail the models and the methods used to analyse them, including bifurcation diagrams and generalized modeling for both bifurcation analysis and early warning signals as well as conventional early warning signals. Section 'Results' presents the results of these bifurcation and early warning signal analyses, and we discuss their implications for modelling studies and for governance of social–ecological systems in Section 'Discussion and implications for management'. Concluding remarks are presented in Section 'Conclusions'.

Methods

We begin by introducing background theory and the analytical tools we propose to use in our analysis, then describe the model to which they will be applied.

Bifurcation theory

Bifurcation theory describes sudden qualitative changes in the dynamical behaviour of systems. Specifically, a bifurcation of a dynamical system occurs when a small, smooth change in a parameter of the dynamical system causes a qualitative change to the dynamics of the system (Kuznetsov 2010). In this article, we analyse the bifurcations of our social–ecological models to understand qualitative changes in their behaviour.

'Fold' bifurcations arise when, as a parameter is varied and passes through a critical point, a stable fixed point collides with an unstable fixed point and both fixed points disappear (Fig. 1). In the ordinary differential equations we use here, a zero eigenvalue of the linearisation (Jacobian) matrix at the fixed point is necessary for a fold bifurcation. In addition, transversality and nondegeneracy conditions must be satisfied to ensure that a fold bifurcation occurs (Kuznetsov 2010). Tests for transversality and nondegeneracy are discussed in Section 'Generalized modeling for bifurcation analysis'.

Fold bifurcations are important because they can lead to regime shifts (Scheffer et al. 2001). Consider a system initially on or near a stable fixed point. Suppose a slow change in an external driver causes the fixed point to undergo a fold bifurcation, the system as a result will undergo a sudden and possibly large change in state to a distant attractor (Kuehn 2011) (in Fig. 1, this is another stable fixed point).

Another way an equilibrium can lose stability is through a Hopf bifurcation, which may (in the case of *supercritical* Hopf bifurcations) lead to a transition to stable oscillatory dynamics. In a Hopf bifurcation, the Jacobian matrix at a fixed point has a complex conjugate pair of eigenvalues that

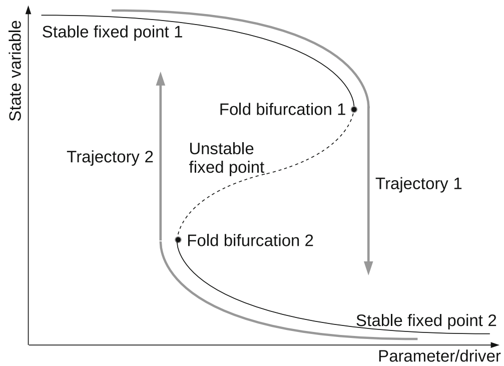

Fig. 1 Bifurcations and regime shifts. Fold bifurcations occur when a stable (*solid lines*) and an unstable (*dashed line*) fixed point collide, and can lead to regime shifts. In the pair of fold bifurcations sketched here (manually, without computer simulation), a system on stable fixed point 1 will, upon the driver passing fold bifurcation 1, undergo a sudden and large shift to stable fixed point 2 (*trajectory 1*). This change is persistent, because the parameter must be returned to a value below fold bifurcation 2 (if this is possible) in order for the system to return to its original state, in another regime shift (*trajectory 2*)

pass through the imaginary axis (hence, have zero real part at the critical value of the parameter) (Kuznetsov 2010).

For simulation models of dynamical systems, where the forms of all interactions and the values of all parameters are known, numerical continuation software are often used to locate and track bifurcations. Here, we used the software XPPAUT (Ermentrout 2011) to plot bifurcation diagrams of the form of Fig. 1, where the values of a parameter or ‘driver’ are plotted on the horizontal axis, and the stable and unstable fixed points of the system corresponding to each value of the driver on the vertical axis.

Generalized modeling for bifurcation analysis

Bifurcation diagrams give great insight into possible qualitative behaviours of the system. Frequently, however, the forms of interactions and the values of parameters in the model on which the bifurcation analysis was performed cannot be accurately known. In a related problem, if functional forms are chosen in a model, there can be significant uncertainty over whether conclusions obtained from the model are of a general nature or are specific to the functional forms chosen.

The generalized modeling approach (Gross and Feudel 2006; Kuehn et al. 2013) can overcome these difficulties. The approach permits precise mathematical statements about bifurcations of a dynamical system to be made despite uncertainties about the functional forms in the dynamical system. Here, we use generalized modeling to make two types of inferences about bifurcations in a dynamical system. The first, and more traditional, use of generalized modeling will be to calculate the types of bifurcations that are permitted by a Generalized model structure. Further below, we use generalized models together with time series data to generate early warning signals for regime shifts.

A generalized modeling bifurcation analysis proceeds as follows:

1. Write down a generalized model structure for the state variables and processes present in the system.
2. Symbolically calculate the Jacobian matrix of a fixed point in this generalized model.
3. Parameterize the Jacobian matrix directly using the so-called generalized parameters. Assign likely ranges of the generalized parameters based on knowledge of the system.
4. Calculate, using appropriate methods, the likely bifurcations to which these values of generalized parameters can lead.

This procedure will be described in further detail below with the aid of a simple example. We also note that the procedure described here above skips the normalisation step often used in previous generalized modeling studies (Gross and Feudel 2006; Kuehn et al. 2013). This leads to the presence of an additional parameter in the Jacobian matrix, which we call the ‘steady-state ratio’ below, but which has no effect on the bifurcation analysis.

Generalized modeling shares its mathematical basis, the bifurcations of dynamical systems, with both the qualitative theory of differential equations (Kelley and Peterson 2010) and catastrophe theory (Zeeman 1977). Indeed, generalized modeling could be considered a systematic way of parameterizing a model before analysing its bifurcations with the tools of qualitative differential equation theory. Two key points of distinction of the generalized modeling are that: (1) it parameterizes the Jacobian matrix directly, rather than the original functional forms; and (2) it provides a systematic framework for connecting a generalized model structure to properties of real systems, through the generalized parameters (see below) or time series observations (in the case of a generalized modeling-based early warning signal). Generalized modeling therefore allows for the investigation of how processes, even incompletely characterised processes, lead to bifurcations of the system. Frequent failure to investigate how system-specific processes could lead to the abstract, general geometries of catastrophes was a major contributor to the controversy over some strands of catastrophe theory (Guckenheimer 1978).

Conceptually, generalized modeling is also similar to systems dynamics approaches (Sterman 2000), structural equation modelling (Kline 2011) and flexible functional forms (Chambers 1988). A generalized model could be considered a causal loop diagram or stock and flow diagram from system dynamics in mathematical form, which we then further manipulate to obtain general mathematical results without resorting to simulating specific systems. Like generalized modeling, structural equation modelling (SEM) explores the consequences of linkages within a network of interacting variables; unlike generalized modeling, SEM can statistically test for the presence and strength of linkages, but does not commonly explore non-linear dynamics and transitions of the variables. In economics, flexible functional forms are a general way to determine functional relationships directly from data, but they generally are not forms that are convenient for a subsequent bifurcation analysis.

For the formulation of a generalized model, the important state variables in the system and the processes through which they interact must first be identified. As a simple example, consider a single population X (which may be of animals, of people, of people holding a particular opinion) that can increase due to a gain process $G(X)$ and decrease due to a loss process $L(X)$, both of which may depend on the current population X. A generalized model, in differential equation form, for the population X is then

$$\frac{\mathrm{d}X}{\mathrm{d}t} = G(X) - L(X). \tag{1}$$

To investigate the bifurcations of this generalized model, we assume that the system has a fixed point, that is, some value X^* where if $X(0) = X^*$ then $X(t) = X^*$ for all $t > 0$. Throughout this article, we use the asterisk to denote a quantity evaluated at the fixed point. We then calculate the Jacobian matrix of the generalized model at the fixed point, and calculate the eigenvalues of the Jacobian matrix, from which we can establish stability and bifurcations as described in Section 'Bifurcation theory'. For Eq. 1, the Jacobian matrix $\mathbf{J}$ consists of a single element which is also the eigenvalue, λ,

$$\mathbf{J} = \lambda = G'^* - L'^*, \tag{2}$$

where the dash denotes a derivative with respect to X. Therefore, to determine the bifurcations of the system, we need to determine the possible ranges of these two derivatives.

To better relate the derivatives in the model to properties of a real-world system, we re-write Eq. 2 in a different form. We introduce:

– the *scale parameter* $\alpha = G^*/X^*$. The parameter α is therefore the per capita inflow rate into the population, which at the fixed point is the same as the per capita outflow rate L^*/X^*. The quantity $\tau = 1/\alpha$ is therefore both the average residence time of an entity in the population and the average time between new entrants (at the fixed point). In this sense, the parameter α sets the characteristic time scale for changes in X.
– the dimensionless *elasticity parameters*

$$G_X = \frac{X^*}{G^*}G'^* \quad \text{and} \quad L_X = \frac{X^*}{L^*}L'^*.$$

The elasticity parameters give an indication of the non-linearity of the process near the fixed point. For example, a linear function $f(x) = ax$ has elasticity 1 for all x. A constant function $f(x) = a$ has elasticity 0 for all x.

The scale and elasticity parameters, and in more complicated examples, another type of parameter called the ratio parameter are collectively referred to as *generalized parameters*, as they are used to represent the dynamics of a general class of models rather than parameterizing a particular model. Using these generalized parameters, Eq. 2 becomes

$$\lambda = \alpha(G_X - L_X),$$

where we have also used the fact that $G^* = L^*$ (see Eq. 1: at the fixed point X^*, $dX/dt = 0$).

Next, we identify what conditions on the generalized parameters can give rise to different types of bifurcations. As described in the previous section, a zero eigenvalue of $\mathbf{J}$ is a necessary condition for a fold bifurcation, while a pair of imaginary conjugate eigenvalues is a necessary condition for a Hopf bifurcation. In the current simple example we conclude that, provided $\alpha > 0$, a fold bifurcation may occur if $G_X = L_X$. Hopf bifurcations are not possible since there is only one eigenvalue, which is real.

To confirm the nature of the fold bifurcation, the transversality and nondegeneracy (Kuznetsov 2010) of the fold should be checked. Transversality of the fold bifurcation of Eq. 1 is easily shown by noting that λ is greater than and less than zero for $G_X > L_X$ and $G_X < L_X$, respectively. Checking nondegeneracy, however, requires extending the generalized modeling approach to consider higher derivatives at the fixed point, which although possible (Zumsande 2011) we do not consider here. For the fold bifurcations of Section Generalized modeling bifurcation analysis below, we instead rely on the bifurcation diagrams calculated for our simulation models as evidence of nondegeneracy.

The final step of the generalized modeling process is to make use of contextual knowledge about the processes to evaluate the likelihood of the identified bifurcations. In this example, suppose we know that the loss process $L(x)$ is approximately linear (elasticity 1), while the gain process $G(X)$ is linear at $X = 0$ (elasticity 1) but saturates at high X (elasticity 0). Therefore, $L_X \approx 1$ and $0 < G_X < 1$ for any non-zero population, so a fold bifurcation is unlikely.

If, however, $G(X)$ took a sigmoidal-type shape (with a quadratic or higher-order shape near $X = 0$), then the elasticity G_X could reach and exceed 1 and a fold bifurcation may be possible.

The generalized model that we analyse below is two-dimensional. For this system, we search for bifurcations by identifying combinations of generalized parameters that satisfy

$$\det \mathbf{J} = 0 \tag{3}$$

for fold bifurcations and

$$\operatorname{tr} \mathbf{J} = 0 \text{ and } \det \mathbf{J} > 0 \tag{4}$$

for Hopf bifurcations, where tr denotes the trace of the matrix.[2]

Early warning signals

Consider a dynamical system that is undergoing noisy fluctuations due to a fast noise forcing. As the dynamical system approaches a fold bifurcation, the standard deviation of these fluctuations, under a linear approximation, diverges to infinity and their autocorrelation increases towards one (Scheffer et al. 2009; Kuehn 2013). Although the linear approximation will not hold arbitrarily close to a fold bifurcation, increasing variance and autocorrelation are two well-known early warning signals that have both been shown to precede regime shifts in simulation studies, in laboratory and field experiments and in data of past regime shifts (Lenton 2012; Scheffer et al. 2012).

We examine whether variance and autocorrelation early warning signals also precede the regime shifts we explore in our social–ecological system. To calculate the early warning signals, we use the R package 'early warnings' (Dakos et al. 2012a) developed by Dakos et al. (2012b). The time series were detrended using a Gaussian filter with a bandwidth of 20, which was found to give a clear signal. Warning signals were calculated using sliding windows of the default length, which is half the length of the time series.

We also explore a third early warning signal, the recently developed generalized modeling-based early warning signal (Lade and Gross 2012). Unlike the variance and autocorrelation approaches, which rely purely on time series data of the system, this approach also makes use of structural knowledge about the system. As the name suggests, the approach begins by constructing a generalized model and

[2]These conditions can be easily derived by noting that the eigenvalues of a two-dimensional Jacobian matrix are $\lambda = \frac{1}{2}\operatorname{tr}\mathbf{J} \pm \frac{1}{2}\sqrt{\operatorname{tr}^2\mathbf{J} - 4\det\mathbf{J}}$. We emphasise that Eq. 4 is only valid in two dimensions; approaches that also work for higher dimensions include the Routh-Hurwitz criteria and the method of resultants (Gross and Feudel 2004).

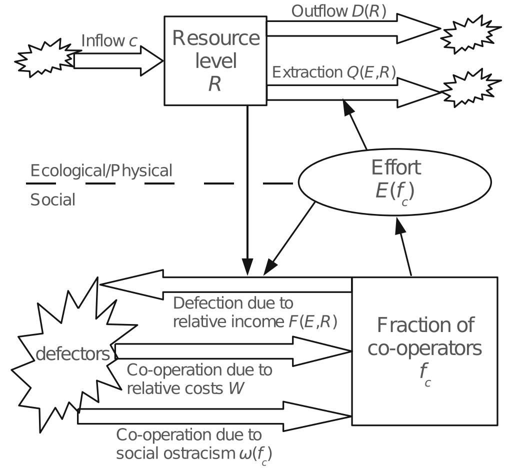

Fig. 2 Schematic of the generalized model Eqs. (5) and (6). Employing some of the systems dynamics conventions (Sterman 2000), we represent flows by *double-line arrows*, influences by *single-line arrows*, state variables by *rectangles*, intermediate quantities by *ovals*, and sources and sinks of flows with *explosion symbols*

then formally calculating its Jacobian matrix as described in the Section 'Generalized modeling for bifurcation analysis'. Instead of assigning ranges to the elements of the Jacobian matrix through generalized parameters, time series observations of the state variables and processes are used to directly estimate the derivatives in the Jacobian matrix. The particular computations used to estimate the derivatives depend on the structure of the generalized model and on the available data; we will derive an algorithm appropriate to the model studied here.

Social ostracism and resource model

We use the tools described above to analyse regime shifts in a stylised social–ecological model (Fig. 2). Our model is a generalized form of the resource and harvester model of Tavoni et al. (2012) (hereafter referred to as the TSL model). We consider a resource, of resource level R, that is being harvested by a community of users. A proportion f_c of the harvesters co-operate to harvest at a socially optimal level while the remaining harvesters 'defect' and harvest at a higher level out of self-interest. We use only two harvesting strategies for analytical tractability; the dynamics of the model with multiple strategies and heterogenous agents is currently being explored in agent-based simulations by some of us (MS, AT, SAL).

We write the resource dynamics in generalized form as

$$\frac{\mathrm{d}R}{\mathrm{d}t} = c - D(R) - Q(E(f_c), R), \tag{5}$$

where c is the resource inflow or growth rate (and is independent of the current resource level), $D(R)$ is the natural resource outflow rate or mortality and $Q(E, R)$ is the resource extraction. Here, $E(f_c)$ is the total effort exerted by the harvesters, which decreases with increasing proportion of co-operators. In practice, the resource could be fish in a fishery, water in an irrigation system, an unpolluted atmosphere, etc.

We, like TSL, use the replicator dynamics of evolutionary game theory to model the dynamics of the fraction of co-operators f_c. In its most general form, the replicator equation for two strategies is $\mathrm{d}f_c/\mathrm{d}t = f_c(1-f_c)(U_c-U_d)$, where U_c and U_d are the utilities for a co-operator and a defector, respectively. In our model, the utilities of defectors and co-operators can differ in three ways.

First, the income received by defectors and co-operators differs due to their harvesting activities, by an amount we denote by $F(E, R) > 0$ that depends on the current resource level R and the total effort E. Second, the costs incurred by defectors and co-operators differ due to their harvesting activities by an amount $W > 0$. We expect both income and costs to be higher for defectors than for co-operators, since defectors invest more effort.

The income difference minus the cost difference constitutes the payoff difference between defectors and co-operators. Like TSL, we include a third difference between co-operator and defector utility: the defectors can be socially ostracised by the co-operators to reduce, by an amount $\omega(f_c) > 0$, the utility of the larger payoff that they would otherwise obtain. Ostracism can occur with the presence of individuals in the community with other-regarding preferences (Fehr and Fischbacher 2002) and when fear of community disapproval leads to pressure to conform with the social norm (Cialdini and Goldstein 2004).

In a minimal approach, norm violaters are identified and ostracised based purely on their payoff, and not discriminated by kin or other relationships. Institutional relationships are indirectly incorporated in the model, however, by allowing the effectiveness of the ostracism $\omega(f_c)$ to increase with the fraction of co-operators f_c. The social capital, expressed in trust and social relationships, needed for effective ostracism of the norm violators can only be built from a large number of norm followers.

That the social ostracism modelled by TSL, which we follow in generalized form here, is non-costly, in that it does not cost the co-operators to impose this punishment. Non-costly ostracism may occur when the community builds upon available social capital (Bowles and Gintis 2002) to deny defectors important services, such as refusing to loan machinery or refusing transportation to market (Tarui et al. 2008; Tavoni et al. 2012). Indeed, sanctioning can even provide benefits to the enforcer (Ostrom 1990). Other models in which co-operation is encouraged in a non-costly manner include those of Osés-Eraso and Viladrich-Grau (2007), Iwasa et al. (2007) and Tarui et al. (2008).

These three differences between co-operator and defector utility result in the following equation for changes in the fraction of co-operators,

$$\frac{\mathrm{d}f_c}{\mathrm{d}t} = f_c(1-f_c)(-F(E(f_c), R) + W + \omega(f_c)). \tag{6}$$

As described in the supporting text, some of our definitions differ from those originally used by TSL. These changes were made in order to reduce Eq. 6 to a number of unknown functions and parameters that is as small as possible while still clearly representing the processes at work in the social–ecological system.

Equations (5) and (6) constitute our generalized model of social ostracism and resource dynamics, hereafter referred to as 'our social–ecological model'. We denote by the ecological or social subsystem the relevant part of the system with any feedback from the other part set to a constant value. It is clear that there are two key processes that link the ecological and social subsystems: extraction of the resource Q, and the income (difference) F gained by harvesters due to extraction (Fig. 2). For both these processes, the effect of the social subsystem is mediated by the total effort E of the harvesting community.

To illustrate or to test our generalized modeling, we will also produce time series data using simulation models. For this purpose, we will use the original TSL model as described in the supporting text and modifications thereof as described below. The TSL model is a specific case of our generalized model; the precise correspondence is shown in the supporting text.

We also use simulations of the TSL model, with added process noise, to test the early warning signals. On R, the noise is purely additive; for f_c, the appropriate Itō noise term has variance proportional to $f_c(1-f_c)$ (Traulsen et al. 2005). During the simulation, which lasted from $t = 0$ to 500, we varied the TSL parameters c and w (see supporting text) according to $c(t) = 40 + 0.024t$ and $w(t) = 18 - 0.08t$. As described in the supporting text, while changing parameters, for simplicity, we do not update, or adapt, the effort levels of defectors and co-operators to the Nash or community-efficient levels for the new parameters. The results of the simulation were sampled at intervals of $\Delta t = 1$ time unit.

Results

Generalized modeling bifurcation analysis

Following the generalized modeling procedure, let there be a fixed point $(R, f_c) = (R^*, f_c^*)$, where $dR/dt = df_c/dt = 0$. Furthermore, we concentrate on mixed-strategy fixed points, $0 < f_c < 1$. Pure strategy ($f_c = 0$

or 1) fixed points also (indeed, always) exist, but we will see below (Fig. 4) that it is usually the bifurcations of the mixed-strategy fixed points that give rise to regime shifts. The Jacobian matrix of the generalized model in Eqs. (5) and (6) evaluated at this fixed point is

$$\mathbf{J} = \begin{bmatrix} -\alpha_R\beta_R D_R - \alpha_R(1-\beta_R)Q_R & -\alpha_R(1-\beta_R)Q_E E_{fc}\delta^R_{fc} \\ -\alpha_f F_R/\delta^R_{fc} & -\alpha_f F_E E_{fc} + \alpha_f(1-\beta_F)\omega_{fc} \end{bmatrix}$$

with the generalized parameters as defined in Table 1.

Using $\mathbf{J}$ and the condition in Eq. 3, we find that for generalized parameters corresponding to the TSL model (Table 1), fold bifurcations are widespread (Fig. 3). Specifically, for any combination of ω_{fc} and D_R in the range plotted, there is an E_{fc} that leads to a fold bifurcation. This matches the bifurcations observed by TSL both in their previous work, as indicated by the appearance and disappearance of their mixed equilibrium states.

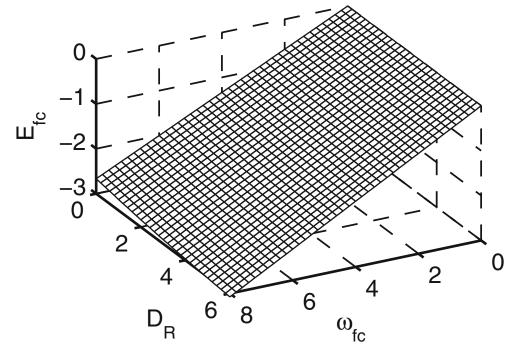

Fig. 3 Generalized modeling analysis. Surface of fold bifurcations for ranges of generalized parameters matching the TSL model. Generalized parameters are set to those used by the TSL model (Table 1) with $\beta_R = 0.1$ and $\beta_F = 0.8$ (the values of α_R and α_f do not affect the position of the fold bifurcation surface). Transversality of the fold bifurcation was confirmed by checking that $d\lambda/d\omega_{fc} \neq 0$ on the surface plotted in the figure, where λ is the dominant eigenvalue. Bifurcation diagrams of the simulation models (Fig. 4), although no general proof, indicate that (in the interior region $0 < f_c < 1$) the fold bifurcations are also nondegenerate. Lastly, we also checked that only one eigenvalue reaches the imaginary axis on the surface of fold bifurcations plotted above

Table 1 Definitions, interpretations and values of the generalized parameters used in the bifurcation analysis. The column 'TSL model' lists the values taken by the generalized parameters for the specific functions and parameterizations used by TSL. For the details of the TSL model and definitions of TSL's k, e_d, e_c, a, b, see the supporting text. The column 'Other values' lists other values given to the generalized parameters during our analysis

Type	Symbol	Definition	Interpretation	TSL value	Other values
Scale	α_R	c/R^*	Fractional rate of replenishment of the c resource from the inflow	0.5 to 2	
	α_f	$-(1-f_c^*)F^*$	Fractional rate of defector recruitment due to income difference F	0 to 0.5	
Ratio	β_R	$D^*/(D^*+Q^*)$	Relative rate of resource loss from outflow compared to harvesting	0.1 to 0.2	
	β_f	$w/(w+\omega_c)$	Relative rate of co-operator recruitment from effort cost compared to ostracism	0.6 to 1	
Elasticity	D_R	Of the form $Y_X \equiv \frac{X^*}{Y^*}Y'^*$	Non-linearity, see Section 'Generalized modeling for bifurcation analysis'	$k = 2$	1, 0 to 6
	Q_R			1	
	Q_E			1	
	E_{f_c}			$1 - e_d/e_c = -2.8$ to 0[a]	
	F_E			$a - 1 = -0.4$	
	F_R			$b = 0.2$	
	ω_{fc}			0 to 8[b]	1
State variable ratio[c]	δ^R_{fc}	R^*/f_c^*	Ratio of state variable values		

[a] The effort elasticity is negative because an increase in co-operators decreases the effort. The elasticity is zero under full defection ($f_c = 0$), because a large fractional change in the number of co-operators leads to a small fractional change in the total effort. In the TSL model, the elasticity takes its largest negative value at full co-operation ($f_c = 1$).

[b] The particular ostracism function chosen by TSL causes the elasticity ω_{fc} to reach extremely high values at values of f_c where the magnitude of the function $\omega(f_c)$ itself is very small. Another function that reproduces TSL's $\omega(f_c)$ very closely is $\omega(f_c) = 0.34 f_c^8/(0.55^8 + f_c^8)$, which has the more reasonable range of elasticities indicated above.

[c] The state variable ratio δ^R_{fc} is not required in any of the following calculations.

Although the Jacobian **J** does permit Hopf bifurcations for some extreme parameter combinations, the Hopf conditions [Eq. (4)] are not simultaneously satisfied anywhere in the generalized parameter space plotted in Fig. 3. We conclude that Hopf bifurcations, and consequently oscillatory states, are unlikely to be observed for models similar to the TSL model.

If we ignore the social dynamics in this system and set the total effort E to a constant, the eigenvalue at a fixed point of R in the ecological subsystem is

$$\lambda_{\mathrm{ecol}} = -\alpha_R \beta_R D_R - \alpha_R (1 - \beta_R) Q_R.$$

Provided that D_R and Q_R are always positive (as they are in the TSL model), this eigenvalue is always negative. Therefore, in this model, no bifurcation can occur and in particular no regime shift can occur. It is clear that by ignoring the social dynamics, it is impossible to appropriately model the regime shift that can occur in our social–ecological system.

To obtain a regime shift in the ecological subsystem alone, D_R or Q_R would have to be sufficiently negative for λ_{ecol} to reach zero. In traditional models of ecological regime shifts, this is achieved because $D(R)$ (or inflow rate, which here is a constant c) is sufficiently non-linear. There are of course many ecological and physical systems with such a regime shift-inducing non-linearity (Scheffer et al. 2001). Our purpose here is to show that regime shifts of ecological states can occur even if the ecological subsystem alone does not have a regime shift.

Returning to Fig. 3, we note, in addition to the ubiquity of fold bifurcations, that (1) fold bifurcations are possible for a large range of ω_{f_c}, including values near 1, and (2) that the presence of fold bifurcations is not strongly affected by the value of D_R. This indicates that close to linear ostracism and resource outflow functions, $\omega(f_c)$ and $D(R)$ may be sufficient to produce a fold bifurcation. We confirm this prediction below using a simulation model.

Furthermore, setting $\omega(f_c) \propto f_c$ and $D(R) \propto R$ removes all non-linearity from both the purely social and purely ecological components of the dynamics. The only remaining non-linearities are contained in the linkage *between* the social and ecological subsystems. This linkage is comprised by the processes $Q(E, R)$, which specifies the amount of resource extracted by the harvesters, and the income difference $F(E, R)$, which specifies the effect of resource extraction on the fraction of co-operators.[3] Thus, as well as arising from non-linearities in the ecological or social dynamics, regime shifts can also arise from non-linearities in the linkages between them.

[3]In the TSL model, these linkages have the following non-linearities: $Q(E, R) \propto ER$ and $F(E, R) \propto E^{a-1} R^b$.

Bifurcations of simulation models

We next tested the general predictions of the generalized modeling analysis above with simulations of the TSL model and variants thereof.

Beginning with the parameter set used by TSL (see supporting text) changing the resource inflow readily triggered a fold bifurcation (Fig. 4a). In fact, changes in any of many different drivers, including effort cost (Fig. 4e), the strength of ostracism (Fig. 4f), or even multiple drivers changing simultaneously (resource inflow and effort cost, Fig. 4g), could trigger the fold bifurcation. We conclude that, as predicted by the generalized modeling analysis, fold bifurcations and therefore regime shifts are easy triggered in our social–ecological model.

Somewhat counter-intuitively, the regime shift from a high co-operation state that led to breakdown of the social norm and collapse of the resource was triggered by an *increasing* resource inflow, countering the common understanding that it is scarcity that leads to conflict. In this model, the regime shift occurred due to an initially increasing resource level that led to a greater increase in the defector income than in co-operator income, due to allocation of net production according to effort. Increased defection then decreased the effectiveness of social ostracism and also increased extraction of the resource, culminating in a collapse in co-operation and in resource levels.

The bifurcation remained (Fig. 4b) when we used a variant of the TSL model with $\omega(f_c) \propto f_c$ and $D(R) \propto R$ (supporting text). The size of the regime shift was not as large as in the case of strongly non-linear $\omega(f_c)$ (Fig. 4a), however. We conclude that, as predicted by the generalized modeling analysis, the presence of the regime shift is robust to the functional form of the ostracism process $\omega(f_c)$, and also to the functional form of the resource outflow $D(R)$. As predicted by the generalized modeling analysis, a simulation model of the ecological subsystem alone, however, did not have a bifurcation (Fig. 4h).

Although the ecological subsystem alone does not display a regime shift, the consequences of the social–ecological regime shift can be just as serious for the resource levels as a purely ecological shift. The regime shift associated with increasing resource inflow (Fig. 4a) led to a significant drop in resource levels (Fig. 4c). The total payoff (income minus costs) that the community received also collapsed (Fig. 4d). In this state, social ostracism is largely ineffective due to the small population of co-operators. Re-establishing the ostracism norm and the associated high resource state would in this model require a large drop in resource inflow, or may even be impossible in the absence of other mechanisms to re-establish the norm.

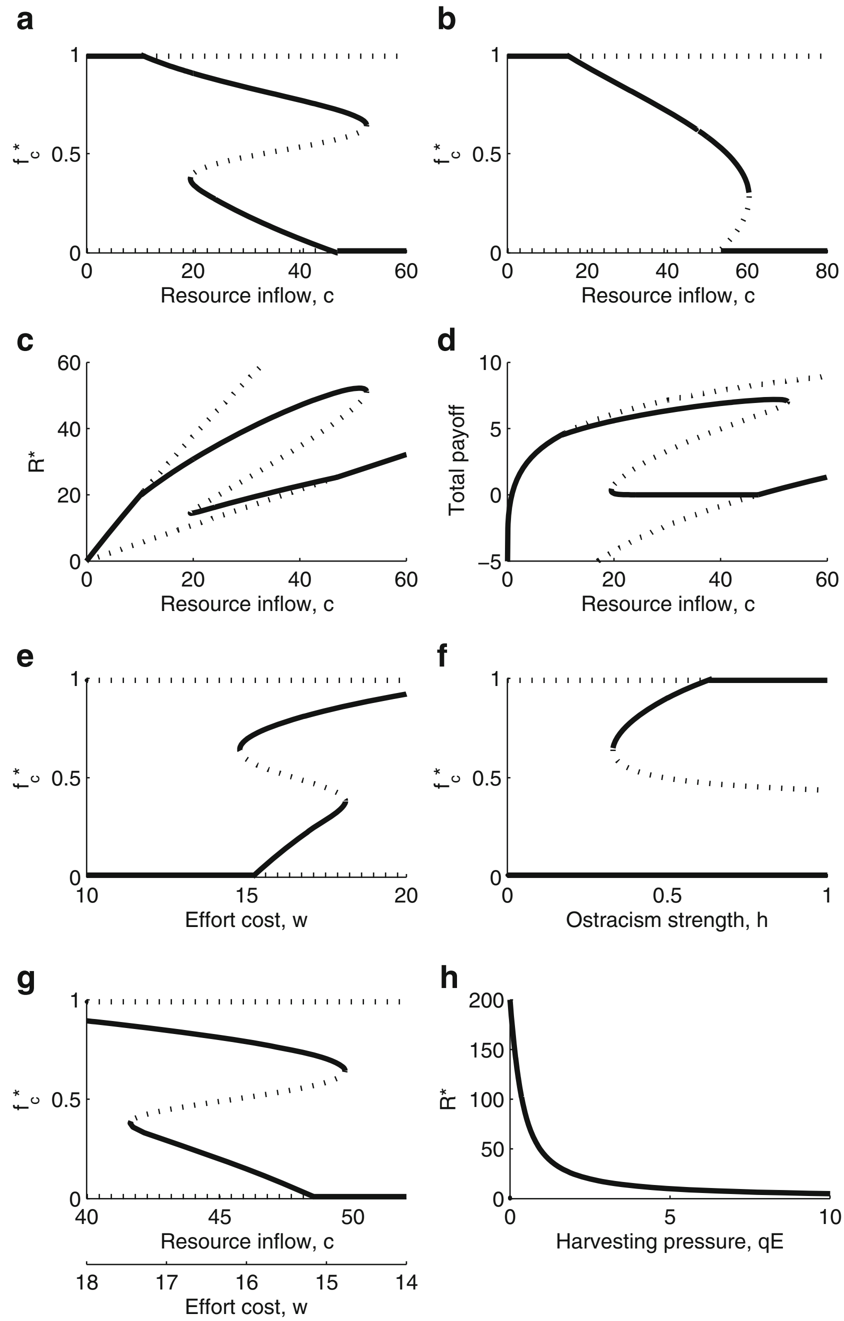

Fig. 4 Bifurcation diagrams of simulation models. The fraction of co-operators f_c are plotted for the fixed points of the TSL model (supporting text) with respect to changes in: **a** the resource inflow; **b** the resource inflow with the functions ω_{fc} and $D(R)$ set to linear forms (see supporting text); **e** the cost of harvesting effort; **f** the strength parameter of the ostracism function; **g** both resource inflow and effort cost at the same time. **h** Fixed points R of the isolated ecological subsystem (supporting text). In **c**, the resource levels and in **d**, the total community payoff $n[f_c^* e_c + (1-f_c^*)e_d][f(E^*, R^*)/E^* - w]$ (see supporting text, for definitions of symbols) corresponding to the fixed points in **a** are shown. *Solid lines* denote stable fixed points, *dotted lines* denote unstable fixed points

Early warning signals

A good standard deviation or autocorrelation warning signal should display a clear upwards trend well in advance of the critical transition. In the early warning literature, these trends in indicators are often quantified with the Kendall τ statistic (Dakos et al. 2012b). The Kendall τ statistic is positive (respectively, negative) if the trend in the time series is upwards (downwards). We applied the standard early warning suite to time series of both R and f_c leading up to the transition (Fig. 5a,b). We observed weak trends in autocorrelation and stronger trends in standard deviation.

We next constructed a generalized modeling-based early warning signal. We assumed that the following quantities could be measured:

– The resource level, R
– The fraction of co-operators, f_c
– The resource outflow, D (for example, natural fish mortality or natural water losses due to evaporation or

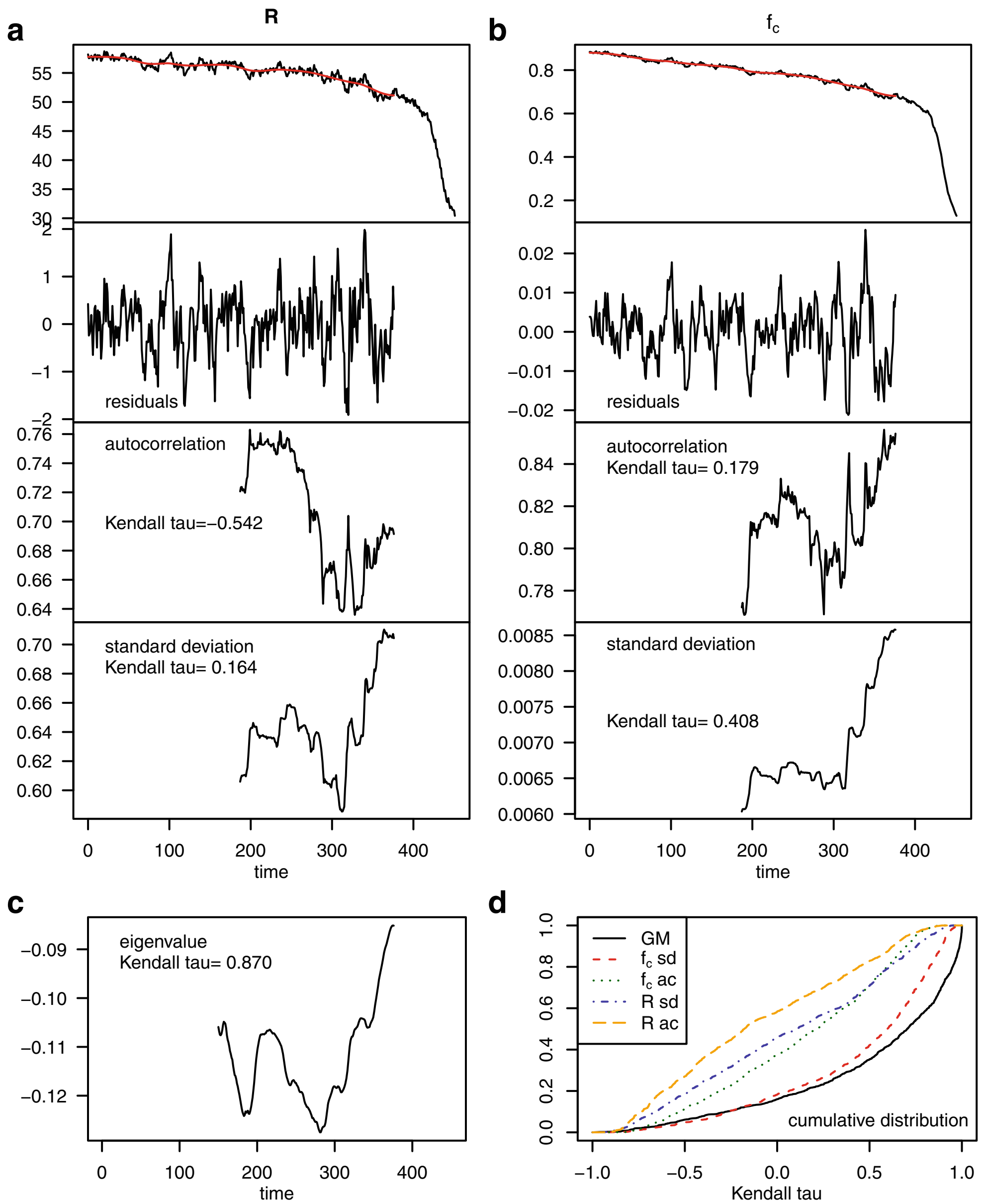

Fig. 5 Early warning signals. **a,b** Time series in the lead-up to a regime shift of our model (*black line*, for parameters of the simulation see text) with filtered fit (*red line*, only over the time range prior to the regime shift to be used in the following analysis); detrended fluctuations; and autocorrelation and standard deviation of the detrended fluctuations. **c** Generalized modeling-based early warning signal preceding the regime shift. **d** Cumulative distributions of the Kendall τ statistics for the different warning indicators (*GM* = generalized modeling-based signal; *ac* = autocorrelation; *sd* = standard deviation) over 1,000 simulations of the regime shift with different noise realisations. All Kendall τ statistics shown were calculated over the time range 300 to 377

outflow), which could be replaced by observations of resource inflow c if more easily measured

- The total resource extraction, Q (for example, total fish caught or total water used for irrigation)
- The income difference between a defector and a co-operator, F
- The cost difference between a defector and a co-operator, W.

We assumed that the regime shift was being triggered by changes in resource inflow c and/or effort costs W. To complete the generalized modeling analysis, we also required the assumptions that: resource extraction is linear in the resource level, $Q \propto R$; and income difference is sub-linear in resource level with known elasticity b, $F \propto R^b$. We found however that the results of the generalized modeling early warning signal are not sensitive to the value of

b used. In the following, we used $b = 0.5$, significantly different from the elasticity actually used in the simulation ($b = 0.2$).

Following the approach outlined by Lade and Gross (2012), we derived an algorithm to calculate the eigenvalues of the generalized model from the quantities in the above list (supporting text). Key outputs of this algorithm included the derivatives of the income difference F, resource extraction Q and ostracism ω with respect to the fraction of co-operators f_c.

From the TSL model with changing parameters described at the end of Section 'Social ostracism and resource model', we generated time series for the list of quantities above. We then applied our algorithm, which yielded time series of two eigenvalues. A clear warning signal would be a negative (stable) eigenvalue increasing consistently towards the stability boundary of zero eigenvalue. The dominant eigenvalue indeed displayed a clear increasing trend (Fig. 5c). The other eigenvalue was always far from the stability boundary, and in fact decreased over the simulation period (from -0.8 to -2).

We also checked the reliability of these early warning signals by repeating the above calculations over an ensemble of realisations of the simulation's regime shift (Fig. 5d). The generalized modeling-based early warning signal and the standard deviation of f_c reliably gave positive Kendall τ statistics. The standard deviation of R and autocorrelations of both f_c and R were not reliable, having median values (cumulative 50 % of distribution) close to zero. On the basis of these results, we find standard deviation of f_c and the generalized modeling eigenvalue to be good candidates for early warning signals for regime shifts in this social–ecological system.

We emphasise, however, that these are preliminary results, and also specific to this social–ecological model. A more thorough analysis would more carefully explore the sensitivity of the observed trends to different algorithm parameters such as smoothing or detrending constants, rolling window size, and time window over which the Kendall τ statistic is calculated (Dakos et al. 2012b) and also consider false alarm and missed detection rates through receiver–operator characteristics (Boettiger and Hastings 2012).

The early warning signal approaches described here also have differing demands on the amount and type of data and knowledge required. The autocorrelation and standard deviation approaches require only high-frequency observations of a single quantity. The generalized modeling-based warning signal, in contrast, requires knowledge of the structure of the social–ecological system as well as regular observations of all state variables and several of the processes by which they interact. It is hoped that, for some regime shifts, such additional, system-specific information will improve the reliability of the warning signal, as well as decreasing the frequency at which time series need to be sampled (Lade and Gross 2012; Boettiger and Hastings 2013).

The generalized modeling approach for early warning signals is also itself in an early stage of development. Future improvements could include statistical approaches: to incorporate partial knowledge about derivatives in the Jacobian matrix; similar to the approach of Boettiger and Hastings (2012), to test the fit of alternative generalized models; and to calculate the level of confidence in an early warning trend.

Discussion and implications for management

In the social–ecological system studied here, the ecological subsystem could not by itself undergo a regime shift at all, whereas regime shifts in the social–ecological system were common. The results of the social–ecological regime shift were as dramatic as purely ecological regime shifts that occur when the human impact acts as a simple driver: there was a rapid, large and persistent collapse of the resource, along with an associated collapse of the social norm and community payoffs. We conclude that failing to model a natural resource as a social–ecological system, which requires including the dynamics of human (and institutional) behaviour, can lead to severely underestimating the potential for regime shifts. In a related result, undesirable regime shifts were previously shown to be avoidable if multiple feedbacks from the state of a complex ecological system were incorporated into management planning (Horan et al. 2011).

The generalized modeling analysis showed that the regime shift persists under variations to the shape of the ostracism function and the natural resource outflows. A regime shift even occurred when the social and ecological subsystems were completely linear, with non-linearities arising only in the extraction and production processes that link the two subsystems. These findings have two implications for natural resource management. First, careful attention should be paid to the links between natural resources and human actors, for example, the way ecosystem services are used and contribute to human well-being. The link between natural resources and human well-being are in particular not well studied. Second, social–ecological systems that under current conditions are managed sustainably through high levels of co-operation, such as the Maine lobster fishery (Acheson and Gardner 2011), could potentially easily be destabilised by small changes in or increasing variability of important processes (see also Steneck et al. 2011). This becomes particularly relevant in the context of global change, where resource dynamics are expected to become more variable or more extreme, thus potentially pushing a successful system rapidly into an unsustainable state.

Indeed, the ease with which a regime shift can be triggered lends support to a precautionary-like approach to managing social–ecological systems (Raffensperger and Tickner 1999): assume the system can undergo regime shifts, unless there is evidence otherwise. Such a precautionary approach may imply, for example: holding stocks at higher levels (Polasky et al. 2011); using generic principles for increasing resilience (Biggs et al. 2012b), such as engaging in a process of adaptive governance; or preparing to mitigate the effects of the regime shift if it is unlikely to be avoided (Crépin et al. 2012).

A complex adaptive systems viewpoint (Levin et al. 2012) is necessary to study regime shifts in social–ecological systems. As well as the possibility of non-equilibrium behaviour (such as regime shifts), an important complex adaptive property of the system we studied here is the ability of human actors to switch their harvesting strategies in response to changing resource levels. The tool of generalized modeling that we have used combines a complex adaptive systems view of the social–ecological system with a precise mathematical setting and the ability to obtain results in the presence of uncertainty about specific forms of interactions. Given the high degree of uncertainty often associated with the detailed workings of social and ecological processes, we anticipate generalized modeling to be a useful tool in future work on social–ecological systems. Although recently developed, generalized modeling (sometimes also called structural kinetic modelling) has already yielded successes in ecology (Gross et al. 2009; Aufderheide et al. 2012), physiology (Zumsande et al. 2011) and molecular biology (Steuer et al. 2006; Gehrmann and Drossel 2010; Zumsande and Gross 2010), where the details of specific interactions can likewise be difficult to determine.

We also studied regime shifts in our social–ecological system using a simulation model. The regime shifts could be triggered by many different social and ecological drivers, and also a combination of drivers. We also obtained the result, on first glance counterintuitive, that *increasing* the resource inflow led to a collapse of co-operation and sudden decrease in the resource level and payoffs, due to the defectors gaining more from an increase in resource level than co-operators. We conclude that sometimes, not only can the regime shift itself be surprising, but the direction of change in a driver that triggers a regime shift can also be surprising.

Given the widespread existence and sometimes surprising nature of these social–ecological regime shifts, some early warning of an impending regime shift would be highly desirable, in order to avoid or at least mitigate the effects of the regime shift. We tested the performance of standard early warning signals for one of the regime shifts produced by the TSL model. The autocorrelation warning signal showed only a weak indication of the transition, with standard deviation (particularly of f_c) and the generalized modeling-based signal showing stronger signals. In practice, the effectiveness of an early warning signal can depend on a number of factors, including: the magnitude of the noise (Contamin and Ellison 2009; Perretti and Munch 2012); appropriate choice of variable(s) to observe; whether a potential associated with the dynamics exists and is smooth (Hastings and Wysham 2010); the rate at which the driver is changing relative to the inherent time scales of the systems, such as life spans (Bestelmeyer et al. 2011); the observation rate compared to these inherent time scales (Bestelmeyer et al. 2011); non-stationary noise statistics (Dakos et al. 2012c); and indeed whether the regime shift is driven at all or is instead triggered by noisy fluctuations (Ditlevsen and Johnsen 2010). The autocorrelation, standard deviation and generalized modeling early warning approaches also have different requirements for the amount and type of data and knowledge required (Section ‘Early warning signals’). We conclude that early warning signal approaches show potential for warning of social–ecological regime shifts, which could be valuable in natural resource management to guide management responses to variable and changing resource levels or changes in resource users. However, investigation of specific cases of social–ecological regime shifts is required to ascertain, first, the availability of the required data in those cases and, second, the robustness of the resulting early warning signals.

A third and very important criterion by which to evaluate an early warning signal in a specific case study is whether the signal can give sufficiently early warning for the transition to be avoided. Successfully averting a transition depends on a number of case-specific factors, including which drivers can be manipulated (Biggs et al. 2009), the rate at which this can be done (Biggs et al. 2009), how fast the system responds to a change in management (Contamin and Ellison 2009), and, importantly, how fast the uncontrolled driver is itself changing. In the limit of a very slowly changing driver, for example, warning signals are likely to provide sufficient notice for action to be taken, while in the limit of a very quickly changing driver, effectively an unpredictable shock, no warning signal could be sufficiently fast. Including management responses in the social–ecological system and evaluating whether warning signals can give sufficient notice for management actions to avert a regime shift are beyond the scope of the stylised models used here. A thorough investigation would require more detailed mechanistic models as well as data pertaining to actual social–ecological regime shifts (Schlüter et al. 2012b).

Conclusions

We studied stylised models of a social–ecological system of broad relevance: a common-pool resource, which is being harvested, and for which a normative mechanism amongst harvesters (social ostracism) encourages a socially optimal harvesting strategy. We found that neglecting the dynamics of the social subsystem of the social–ecological system led to models missing the existence of regime shifts in the system, regime shifts which could be as persistent and economically detrimental as a purely ecological regime shift. Furthermore, we found the regime shift to be robust to uncertainty about the specific shapes of the interaction processes, leading us to support the inclusion of regime shifts within a precautionary approach to managing ecosystems. Finally, we also showed that the early warning signals developed for ecological or physical systems may also be useful for anticipating regime shifts in social–ecological systems.

Acknowledgments The authors would like to thank Oonsie Biggs, Ralf Eichhorn, Carl Folke, Thilo Gross, Jamila Haider, Juan Carlos Rocha and Nanda Wijermans for helpful comments on the manuscript. The research leading to these results has received funding from the European Research Council under the European Unions Seventh Framework Programme (FP/2007-2013)/ERC grant agreement no. 283950 SES-LINK and a core grant to the Stockholm Resilience Centre by Mistra. AT is supported by the Centre for Climate Change Economics and Policy, which is funded by the UK Economic and Social Research Council and Munich Re. SAL was supported by National Science Foundation grants EF-1137894 and GEO-1211972.

References

Acheson J, Gardner R (2011) The evolution of the Maine lobster V-notch practice: cooperation in a prisoner's dilemma game. Ecol Soc 16:41

Aufderheide H, Rudolf L, Gross T (2012) Mesoscale symmetries explain dynamical equivalence of food webs. New J Phys 14(10):105014

Berkes F, Folke C (1998) Linking social and ecological systems Management practices and social mechanisms for building resilience. Cambridge University Press, Cambridge

Bestelmeyer BT, Ellison AM, Fraser WR, Gorman KB, Holbrook SJ, Laney CM, Ohman MD, Peters DPC, Pillsbury FC, Rassweiler A, Schmitt RJ, Sharma S (2011) Analysis of abrupt transitions in ecological systems. Ecosphere 2:129

Biggs R, Carpenter SR, Brock WA (2009) Turning back from the brink: detecting an impending regime shift in time to avert it. Proc Natl Acad Sci USA 106(3):826–831

Biggs R, Blenckner T, Folke C, Gordon L, Norström A, Nyström M, Peterson G (2012a) Regime shifts. In: Hastings A, Gross LJ (eds) Encyclopedia of theoretical ecology. University of California Press, Berkeley, pp 609–617

Biggs R, Schlüter M, Biggs D, Bohensky EL, BurnSilver S, Cundill G, Dakos V, Daw TM, Evans LS, Kotschy K, Leitch AM, Meek C, Quinlan A, Raudsepp-Hearne C, Robards MD, Schoon ML, Schultz L, West PC (2012b) Toward principles for enhancing the resilience of ecosystem services. Annu Rev Environ Resour 37:421–448

Boettiger C, Hastings A (2012) Quantifying limits to detection of early warning for critical transitions. J R Soc Interface 9:2527–2539

Boettiger C, Hastings A (2013) From patterns to predictions. Nature 493:157–158

Bowles S, Gintis H (2002) Social capital and community governance. Econ J 112(483):F419–F436

Carpenter SR, Mooney HA, Agard J, Capistrano D, DeFries RS, Daz S, Dietz T, Duraiappah AK, Oteng-Yeboah A, Pereira HM, Perrings C, Reid WV, Sarukhan J, Scholes RJ, Whyte A (2009). Proc Natl Acad Sci 106(5):1305–1312

Chambers RG (1988) Applied production analysis: a dual approach. Cambridge University Press, Cambridge

Cialdini RB, Goldstein NJ (2004) Social influence: compliance and conformity. Annu Rev Psychol 55:591–621

Contamin R, Ellison AM (2009) Indicators of regime shifts in ecological systems: what do we need to know and when do we need to know it. Ecol Appl 19:799–816

Crépin AS, Lindahl T (2009) Grazing games: sharing common property resources with complex dynamics. Environ Resour Econ 44:29–46

Crépin AS, Biggs R, Polasky S, Troell M, de Zeeuw A (2012) Regime shifts and management. Ecol Econ 84:15–22

Dakos V, Carpenter S, Cline T, Lahti L (2012a) Early warning signals toolbox. Version 1.0.2, http://earlywarnings.r-forge.r-project.org

Dakos V, Carpenter SR, Brock WA, Ellison AM, Guttal V, Ives AR, Kfi S, Livina V, Seekell DA, van Nes EH, Scheffer M (2012b) Methods for detecting early warnings of critical transitions in time series illustrated using simulated ecological data. PLoS ONE 7(7):e41010

Dakos V, van Nes EH, D'Oderico P, Scheffer M (2012c) Robustness of variance and autocorrelation as indicators of critical slowing down. Ecol 93:264–271

Ditlevsen PD, Johnsen SJ (2010) Tipping points: early warning and wishful thinking. Geophysical Research Letters 37(19):L19703

Ermentrout B (2011) XPPAUT. Version 6.11, http://www.math.pitt.edu/∼bard/xpp/xpp.html

Fehr E, Fischbacher U (2002) Why social preferences matter—the impact of non-selfish motives on competition, cooperation, and incentives. Econ J 112(478):C1–C33

Folke C, Carpenter SR, Walker B, Scheffer M, Chapin T, Rockström J (2010) Resilience thinking: integrating resilience, adaptability and transformability. Ecol Soc 15:20

Gehrmann E, Drossel B (2010) Boolean versus continuous dynamics on simple two-gene modules. Phys Rev E 82:046120

Gross T, Feudel U (2004) Analytical search for bifurcation surfaces in parameter space. Physica D 195(34):292–302

Gross T, Feudel U (2006) Generalized models as a universal approach to the analysis of nonlinear dynamical systems. Phys Rev E 73(1):016205

Gross T, Rudolf L, Levin SA, Dieckmann U (2009) Generalized models reveal stabilizing factors in food webs. Science 325:747–750

Guckenheimer J (1978) The catastrophe controversy. Math Intell 1:15–20

Hastings A, Wysham DB (2010) Regime shifts in ecological systems can occur with no warning. Ecol Lett 13:464–472

Horan RD, Fenichel EP, Drury KLS, Lodge DM (2011) Managing ecological thresholds in coupled environmental-human systems. Proc Natl Acad Sci USA 108:7333–7338

Iwasa Y, Uchida T, Yokomizo H (2007) Nonlinear behavior of the socio-economic dynamics for lake eutrophication control. Ecol Econ 63(1):219–229

Kelley WG, Peterson AC (2010) The theory of differential equations: classical and qualitative, 2nd edn. Springer, New York

Kline RB (2011) Principles and Practice of structural equation modeling, 3rd edn. Guilford Press, New York

Kuehn C (2011) A mathematical framework for critical transitions: bifurcations, fast-slow systems and stochastic dynamics. Physica D 240:1020–1035

Kuehn C (2013) A mathematical framework for critical transitions: normal forms, variance and applications J Nonlinear Sci. doi:10.1007/s00332-012-9158-x

Kuehn C, Siegmund S, Gross T (2013) Dynamical analysis of evolution equations in generalized models. IMA J Appl Math. doi:10.1093/imamat/hxs008

Kuznetsov Y (2010) Elements of applied bifurcation theory. Springer, New York

Lade SJ, Gross T (2012) Early warning signals for critical transitions: a generalized modeling approach. PLoS Comput Biol 8(2):e1002360

Lenton TM (2012) What early warning systems are there for environmental shocks?. In press

Levin S, Xepapadeas T, Crépin AS, Norberg J, de Zeeuw A, Folke C, Hughes T, Arrow K, Barrett S, Daily G, Ehrlich P, Kautsky N, Mäler KG, Polasky S, Troell M, Vincent JR, Walker B (2012) Social-ecological systems as complex adaptive systems: modeling and policy implications. Environ Dev Econ FirstView: 1–22

Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: synthesis. Island Press, Washington DC

Osés-Eraso N, Viladrich-Grau M (2007) On the sustainability of common property resources. J Environ Econ Manag 53(3):393–410

Ostrom E (1990) Governing the commons: the evolution of institutions for collective action. Cambridge University Press, Cambridge

Ostrom E (2006) The value-added of laboratory experiments for the study of institutions and common-pool resources. J Econ Behav Organ 61(2):149–163

Perretti CT, Munch SB (2012) Regime shift indicators fail under noise levels commonly observed in ecological systems. Ecol Appl 22:1771–1779

Polasky S, de Zeeuw A, Wagener F (2011) Optimal management with potential regime shifts. J Environ Econ Manag 62(2):229–240

Raffensperger C, Tickner J (1999) Protecting public health and the environment Implementing the precautionary principle. Island Press, Washington DC

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413:591–596

Scheffer M, Bascompte J, Brock WA, Brovkin V, Carpenter SR, Dakos V, Held H, van Nes EH, Rietkerk M, Sugihara G (2009) Early-warning signals for critical transitions. Nature 461:53–59

Scheffer M, Carpenter SR, Lenton TM, Bascompte J, Brock W, Dakos V, van de Koppel J, van de Leemput IA, Levin SA, van Nes EH, Pascual M, Vandermeer J (2012) Anticipating critical transitions. Science 338:344–348

Schlüter M, McAllister RRJ, Arlinghaus R, Bunnefeld N, Eisenack K, Hölker F, Milner-Gulland E, Müller B, Nicholson E, Quaas M, Stöven M (2012a) New horizons for managing the environment: a review of coupled social-ecological systems modeling. Nat Resour Model 25:219–272

Schlüter M, Müller B, Frank K (2012b) MORE—modeling for resilience thinking and ecosystem stewardship. Available at SSRN: http://ssrn.com/abstract=2037723 or http://dx.doi.org/10.2139/ssrn.2037723

Steneck RS, Hughes TP, Cinner JE, Adger WN, Arnold SN, Berkes F, Boudreau SA, Brown K, Folke C, Gunderson L, Olsson P, Scheffer M, Stephenson E, Walker B, Wilson J, Worm B (2011) Creation of a gilded trap by the high economic value of the maine lobster fishery, vol 25

Sterman JD (2000) Business Dynamics: Systems Thinking and Modeling for a Complex World. McGraw-Hill

Steuer R, Gross T, Selbig J, Blasius B (2006) Structural kinetic modeling of metabolic networks. Proc Natl Acad Sci 103(32):11868–11873

Tarui N, Mason CF, Polasky S, Ellis G (2008) Cooperation in the commons with unobservable actions. J Environ Econ Manag 55(1):37–51

Tavoni A, Schlüter M, Levin S (2012) The survival of the conformist: social pressure and renewable resource management. Journal of Theoretical Biology 299:152–161

Traulsen A, Claussen JC, Hauert C (2005) Coevolutionary dynamics: from finite to infinite populations. Physical Review Letters 238701:95

Zeeman EC (1977) Catastrophe theory: selected papers, 1972–1977. Addison-Wesley

Zumsande M (2011) Extension of generalized modeling and application to problems from cell biology. PhD thesis, Technische Universität Dresden

Zumsande M, Gross T (2010) Bifurcations and chaos in the MAPK signaling cascade. J Theor Biol 265(3):481–491

Zumsande M, Stiefs D, Siegmund S, Gross T (2011) General analysis of mathematical models for bone remodeling. Bone 48(4):910–917