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Boerlijst, M.C.; Oudman, T.; de Roos, A.M.

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Catastrophic Collapse Can Occur without Early Warning: Examples of Silent Catastrophes in Structured Ecological Models

Maarten C. Boerlijst*, Thomas Oudman**, André M. de Roos

Introduction

Catastrophic regime shifts can occur in many ecosystems, and often such shifts cause substantial loss of biodiversity and ecosystem functioning [1]. Recently, the existence of generic early warning signals, which precede and can predict such a catastrophic collapse, has received much attention [2][3][4][5][6][7], although the concept was already proposed much earlier [8]. Already in the seventies of the last century it was pointed out that catastrophic ecosystem collapses can be caused by an underlying fold bifurcation [9][10]. Figure 1 shows such a so-called “catastrophe fold”, where, near the bifurcation points $T_1$ and $T_2$, a slight change in the environmental conditions can cause a sudden shift from one stable state to another. As catastrophic shifts can cause substantial loss of biodiversity and ecosystem functioning, reliably predicting such catastrophes would be of crucial importance. Recently, it has been proposed that there exist generic early warning signals, based on a phenomenon that is coined “critical slowing down” near the bifurcation [6]. At the fold bifurcation, the eigenvalue of the dominant eigenvector becomes zero, and consequently, near the bifurcation, perturbations in the direction of this eigenvector only very slowly return to the equilibrium. As a result, the variance and autocorrelation will both steeply increase when approaching the fold bifurcation. This is a generic property of fold bifurcations, and it suggests that indeed generic early warning signals can be observed for natural ecosystems [7][11][12]. However, how robust and informative these early warning signals are for more complex ecosystems remains unclear.

Abstract

Catastrophic and sudden collapses of ecosystems are sometimes preceded by early warning signals that potentially could be used to predict and prevent a forthcoming catastrophe. Universality of these early warning signals has been proposed, but no formal proof has been provided. Here, we show that in relatively simple ecological models the most commonly used early warning signals for a catastrophic collapse can be silent. We underpin the mathematical reason for this phenomenon, which involves the direction of the eigenvectors of the system. Our results demonstrate that claims on the universality of early warning signals are not correct, and that catastrophic collapses can occur without prior warning. In order to correctly predict a collapse and determine whether early warning signals precede the collapse, detailed knowledge of the mathematical structure of the approaching bifurcation is necessary. Unfortunately, such knowledge is often only obtained after the collapse has already occurred.

Methods

In this paper, we investigate a simple ecological model for the interaction between a predator and a stage-structured prey species. The model distinguishes between juvenile and adult prey individuals, and the predator only attacks adult prey. The model, in its most general form, consists of three ordinary differential equations for, respectively, juvenile ($J$), adult ($A$), and predator density ($P$):

$$\frac{dJ}{dt} = f(A) - g(J) - \mu_J J; \quad \frac{dA}{dt} = g(J) - h(A, P) - \mu_A A;$$

$$\frac{dP}{dt} = h(A, P)c - \mu_P P$$

Here, $f(A)$ is a function that specifies the reproduction rate of adults, $g(J)$ specifies the maturation rate of juveniles, and $h(A, P)$ is the predation rate on adults. Parameters $\mu_A, \mu_J, \mu_P$ are death rates, and $c$ is a conversion factor. We use a realization of this model with $f(A) = hA$, $g(J) = J/(1+J^2)$, and $h(A, P) = AP$. For a description of the ecological setting of the model we refer to an earlier paper by van Kooten et al. [13]. Predation and fecundity are linear functions, and maturation is non-linear. In absence of predators the prey population is regulated by a maturation bottleneck at high juvenile density. Parameter $b$ represents adult reproduction rate. Environmental noise is added to this model by randomly varying death rates every time unit, applying random (white), or correlated (pink) noise. This method of adding noise to...
the per capita death rates is giving similar results to directly perturbing population numbers after every time unit. For numerical integration we used the Cash-Karp Runge-Kutta method [14] for solving ordinary differential equations.

Results

In Figures 2A through 2D, we gradually increase the predator death rate towards the catastrophic collapse of the predator density at \( \mu_p = 0.553 \) (corresponding to point \( T_1 \) in Figure 1), and we monitor the coefficient of variation for all three state variables.
Notably, no early warning signal is observed for the variation in adult and predator density, regardless of the way in which environmental noise is added to the system. This is striking, because the predator is the species that will collapse at the catastrophe, and yet, it is not displaying any warning signal. There can be an early warning sign in the juvenile density, but only if noise is applied to the juvenile population (Figure 2A), or if noise is added independently to all three populations (Figure 2C). Most surprisingly, the catastrophic collapse happens without any prior warning if environmental noise is applied to the adult population (Figure 2B) or to all three populations in a correlated manner (Figure 2D). The latter procedure corresponds to a situation where changing environmental conditions affect all three populations equally. In Figures 3A through 3D it is shown that also autocorrelation does not provide reliable early warning signals for this system. In case of noise on the adult population (Figure 3B)

**Figure 3. Early warning signals in autocorrelation.** For the same simulation as in Figure 2, the lag-1 autocorrelation is computed over the last 50,000 time units. (A) Noise added to the death rate of the juvenile population (B). Noise added to the death rate of the adult population (C). Independent noise added to the death rates of all three populations. (D) Identical, fully correlated, noise added to the death rates of all three populations. For description of the simulation and for color index see Figure 2.

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**Figure 4. Effect of the direction of perturbation on early warning signals.** Predator death rate is fixed at $\mu_p = 0.55$ (close to the catastrophe), and the death rate of either the juveniles or the adults is perturbed using white noise with standard deviation $\sigma = 0.005$. System trajectories are plotted in blue for 60 time units. The dominant eigenvector is indicated by the red arrow, and the second and third eigenvector are indicated by the black arrows. (A) When the juvenile death rate is perturbed, the system responds only in the direction of the dominant eigenvector, resulting in an early warning signal that is only apparent in juvenile population fluctuations. (B) When the adult death rate is perturbed, the system responds in the direction of the surface spanned by the second and third eigenvector (indicated in grey), resulting in damped oscillations and absence of early warning. For other model parameters see Figure 1. For an animated rotation of these 3D figures, and for direction and scaling of axis see Movie S1 and S2.

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and fully correlated noise (Figure 3D) all autocorrelations are
decreasing towards the catastrophe. In case of noise on juveniles
(Figure 3A) or independent noise to all variables (Figure 3C), a
clear early warning signal again only occurs in the juvenile
population.

Apparently, the early warning signals are not generic at all, as a
fold catastrophe can occur without prior warning. So, what is
flawed in the argument that “critical slowing down” is a generic
property of all fold bifurcations? In fact, the statement is
completely correct, but the slowing down only occurs in the
direction of the dominant eigenvector. In our system, this
eigenvector, near the bifurcation, almost exclusively points in the
direction of the axis corresponding to the juvenile population.

Figure 4A shows that adding noise to the juvenile population will
result in the system responding only in the direction of this
dominant eigenvector, causing the early warning signal in the
juvenile density. In contrast, in Figure 4B, when noise is added
to the adult population, perturbations mainly develop in the direction
of the second and third eigenvector. The eigenvalues pertaining to
these eigenvectors are imaginary, and their real parts become
more negative towards the catastrophe, causing increasingly
damped oscillations and absence of critical slowing down. As a
consequence, the forthcoming collapse is camouflaged. We also
examined the linear stability of the system by using the Jacobian
matrix (see [7]). Adding noise to the linearized system gives a very
similar early warning signature in approaching the bifurcation. In
Figure 5A and 5B the linearized system is brought very close to the
bifurcation ($m_p=0.5528$). In Figure 5A, where noise is added
to the juvenile population, this population is clearly showing critically
slowing down, with very large and slow excursions from the
equilibrium, whereas the adult and predator population do not
show an early warning signal. In contrast, in Figure 5B, where the
same amount of noise is added to the adult population, early
warning signals are completely absent from all three populations.

We extensively tested robustness of the silent collapse phenom-
enon, e.g. by varying the type of noise. In Figure 6A, more natural

![Figure 5. Early warning signals in the linearized system.](image)

**Figure 5. Early warning signals in the linearized system.** The model of Figure 1 is linearized using the Jacobian matrix. Predator death rate is set at $\mu_p=0.5528$ (very close to the bifurcation point $T_1$ in Figure 1). The death rate of either the juveniles or the adults is perturbed using white noise with standard deviation $\sigma=0.005$. (A) When noise is added to the juvenile death rate, the juvenile population (indicated in blue) clearly shows critically slowing down, whereas the adult (green line) and predator (red line) populations do not show early warning signs. (B) When noise is added to the adult death rate, all three populations do not show any sign of early warning. Note that the fluctuations in the juvenile population in Figure 5A are so large, that the full (i.e. not linearized) system would shift to the alternative steady state.

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![Figure 6. Early warning signals with correlated noise and discrete noise.](image)

**Figure 6. Early warning signals with correlated noise and discrete noise.** Coefficient of variation and autocorrelation are monitored for increasing predator death rate towards the catastrophic collapse at $\mu_p=0.553$. Bifurcation procedure, parameters and colors are identical to Figure 2. (A) Coefficient of variation when pink noise (1/f correlated noise) is added to the death rate of the adult population. (B) Coefficient of variation when discrete white noise is applied directly to the adult population numbers after each time step.

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correlated ‘pink’ noise [15] is added to the death rate of the adult population (using the method of Vasseur and Yodzis [16]). The correlated noise is increasing the system variance, but the approach to the catastrophe remains completely silent. In Fig 6B, discrete white noise is, after each time unit, directly applied to the adult population numbers. Also with this type of noise the approach to the catastrophe is not showing any early warning signals. We furthermore investigated the presence of early warning signals near the second bifurcation point in our system (i.e. $T_2$ in Figure 1). Also in this case adding noise on the adult population results in a silent approach to the catastrophe. Finally, we have investigated the presence of early warning signals for each value of $m_P$ over the last 40,000 time steps. (A) Coefficient of variation, and (B) Autocorrelation. All other parameters have default values as used by de Roos and Persson [17].

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We have focused on catastrophic regime shifts that are caused by an underlying fold bifurcation, as this cause of bistability has received most attention in the ecological literature. However, catastrophic shifts can also be induced by other underlying mathematical structures, such as a subcritical Hopf bifurcation or a bifurcation to a chaotic attractor. For this latter possibility it has recently been demonstrated that also in this case early warning signals can be absent [23]. Furthermore, early warning can be weak if environmental noise is coupled to a system parameter that has a decreasing contribution to the dynamics when approaching the catastrophe [24]. To even further limit the predictive value of early warning signals, these signals can also occur in approaching other, non-catastrophic, bifurcations, such as a Hopf or a transcritical bifurcation [25]. Also, transient dynamics resulting from e.g. changing environmental conditions can generate early warning signals without a forthcoming collapse. In conclusion, we propose to reject the currently popular hypothesis that catastrophic shifts are preceded by universal early warning signals. We have provided counterexamples of silent catastrophes, and we have pointed out the underlying mathematical reason for the absence of early warning signals. In order to assess whether specific early
warning signals will occur in a particular system, detailed knowledge of the underlying mathematical structure is necessary. Using early warning signals as a tool for nature conservation could still prove to be a good general policy, but it definitely needs more theoretical underpinning.

Supporting Information

Movie S1 Animated rotation of Figure 4A. White noise is added to the juvenile prey death rate, which induces excursions of the system state in the direction of the dominant eigenvector (indicated by the red arrow). As a result, the system only responds along this eigenvector (trajectory in blue), leading to an early warning signal that only appears in the juvenile population.

(MOV)

Movie S2 Animated rotation of Figure 4B. White noise is added to the adult prey death rate, which induces excursions of the system state in the direction of the surface (indicated in grey) corresponding to the second and third eigenvector (black arrows). As a result, the system responds with damped oscillations (trajectory in blue), leading to a total absence of early warning signals.

(MOV)

Author Contributions

Conceived and designed the experiments: MCB TO AMdR. Performed the experiments: MCB TO AMdR. Analyzed the data: MCB TO AMdR. Wrote the paper: MCB.

References