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Slow Recovery from Perturbations as a Generic Indicator of a Nearby Catastrophic Shift

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ABSTRACT: The size of the basin of attraction in ecosystems with alternative stable states is often referred to as "ecological resilience." Ecosystems with a low ecological resilience may easily be tipped into an alternative basin of attraction by a stochastic event. Unfortunately, it is very difficult to measure ecological resilience in practice. Here we show that the rate of recovery from small perturbations (sometimes called "engineering resilience") is a remarkably good indicator of ecological resilience. Such recovery rates decrease as a catastrophic regime shift is approached, a phenomenon known in physics as "critical slowing down." We demonstrate the robust occurrence of critical slowing down in six ecological models and outline a possible experimental approach to quantify differences in recovery rates. In all the models we analyzed, critical slowing down becomes apparent quite far from a threshold point, suggesting that it may indeed be of practical use as an early warning signal. Despite the fact that critical slowing down could also indicate other critical transitions, such as a stable system becoming oscillatory, the robustness of the phenomenon makes it a promising indicator of loss of resilience and the risk of upcoming regime shifts in a system.

Keywords: alternative stable states, catastrophic bifurcations, critical slowing down, early warning signals, resilience, return time.

Evidence is accumulating that some large-scale complex systems may have alternative equilibria and critical tipping points. This seems to be true for a range of ecosystems but also for other systems, including climate (Higgins et al. 2002; Alley 2004; Kump 2005) and socioeconomic sys-

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tems (Brock and Durlauf 1999; Gladwell 2000; Adler 2001; Scheffer et al. 2003). It is difficult to prove experimentally that a system has multiple stable states (Scheffer and Carpenter 2003; Schröder et al. 2005), but the implications are profound if this phenomenon occurs in a system. A major problem from a management point of view is that slowly changing conditions can make such systems increasingly vulnerable to collapse into an alternative state. This typically happens in an invisible way, that is, without apparent effects on the state of the system. Such loss of resilience arises if the basin of attraction around the present state shrinks, making it increasingly likely that some stochastic event will tip the system into an alternative basin of attraction (fig. 1a, 1b). As an intuitive example, consider being in a canoe and leaning over to one side to see something under water. Leaning over too much may cause the canoe to capsize and end up in an alternative stable state, upside down. It is difficult to see the tipping point coming, as the position of the boat may change relatively little up until the critical point. Moreover, close to the tipping point, small disturbances such as waves can tip the balance.

Obviously, the ability to absorb perturbations without being pushed into an alternative basin of attraction is an important measure of the stability of a system (fig. 1a, 1b). For this concept, Holling (1973) suggested using the term "resilience." Unfortunately, this term is often also used for another aspect of stability, namely, the return rate to equilibrium after a small perturbation (Pimm 1984; fig. 1c, 1d), an aspect referred to as "engineering resilience" by Holling (1996). To avoid confusion (Grimm and Wissel 1997) in this article, we will use the term "ecological resilience" for the width of the basin of attraction (Holling 1973) and the term "recovery rate" for the return rate after a disturbance to equilibrium (Pimm 1984).

It has been argued that good management strategies for systems with alternative basins of attraction should be aimed at preserving or enhancing ecological resilience (the width of the basin of attraction of the preferred state), as this can usually be better controlled than stochastic events that may trigger unwanted shifts (Scheffer et al. 2001). However, a major problem is that ecological resilience can-
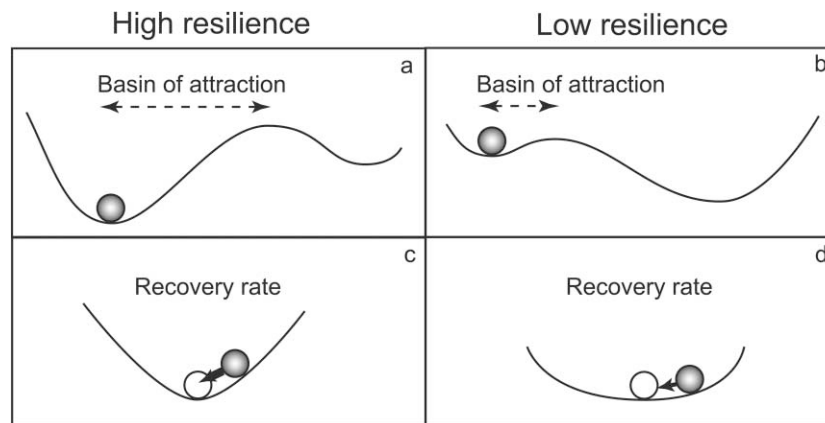
Figure 1: Stability properties of an ecosystem can be intuitively depicted by the fate of a ball in a landscape of hills and valleys. The size of the basin of attraction is a measure of the maximal disturbance that a system can absorb without shifting to another state (*a*, *b*). This property is often referred to as "ecological resilience" (Holling 1996). The recovery rate from a small perturbation (*c*, *d*) is a measure of local stability of an equilibrium. As we show in the text, such local recovery rates reflect the size of the basin of attraction even if the perturbation does not bring the system close to the border of the attraction basin.

not be measured in practice. Therefore, there is a great need for indirect indicators of ecological resilience (Carpenter et al. 2001). The most common approach has been to use models to determine specific indicators of ecological resilience (Carpenter et al. 2001; Bennett et al. 2005). However, the results of such models are rather uncertain, and often the exact mechanisms of regime shifts are poorly known (e.g., Hare and Mantua 2000). Therefore, it would be helpful to develop generic indicators that can be measured directly. Recently, two potential indicators have been proposed that are related to the phenomenon that, close to a threshold point, the signal of fluctuation in the state variables tends to change. Kleinen et al. (2003) showed for a stochastic climatic model that the signal becomes more autocorrelated close to the threshold point (= "redder"). Carpenter and Brock (2006) used a stochastic lake model to show that variance of the state variables will increase close to the threshold.

Here, we explore a third generic type of indicator of an upcoming threshold, known in physics as "critical slowing down" (Strogatz 1994). This phenomenon refers to the fact that in continuous models, recovery rates approach zero as the size of the basin of attraction shrinks to nil (at the threshold; Wissel 1984). Critical slowing down has rarely been referred to in ecology (Rietkerk et al. 1996; Gandhi et al. 1998). However, it has been demonstrated in a relatively realistic model of thermohaline oceanic circulation approaching a catastrophic threshold (Held and Kleinen 2004).

We explore whether critical slowing down could be used an indicator of ecological resilience. We demonstrate the phenomenon in a set of four simple and two complex

ecological models. Finally, we discuss how generic this result is and under which conditions it could be a useful indicator in practice.

Models

To probe the relationship between recovery rate and the width of the basin of attraction, we first analyze how those two properties change as a catastrophic threshold is approached in six published models of systems with alternative stable states (parameters and equations in table 1). The first model has one differential equation and describes the effect of grazing pressure on a population that grows logistically (Noy-Meir 1975; May 1977). It has been applied to numerous problems of overexploitation of various populations. The second model is also a single differential equation and describes the loss of phosphorus from the top layers (epilimnion) of a deep lake and the sudden recycling if the deeper water (hypolimnion) becomes anoxic (Carpenter et al. 1999). The third model consists of two coupled differential equations and describes the feedback between submerged macrophytes and phytoplankton in a shallow lake (Scheffer 1998; van Nes and Scheffer 2005). The fourth model is the classical Lotka-Volterra model of competition between two species (Lotka [1925] 1956; Edelstein-Keshet 1988) for the situation when coexistence is unstable (interspecific competition is greater than intraspecific competition). The fifth model is a multispecies version of the competition model that includes the effect of an environmental factor (van Nes and Scheffer 2004). We used a pool of 20 competing species with ran-

Table 1: Overview of the models and parameters that were used

Model	Parameters	Description and references
$\frac{dX}{dt} = rX\left(1 - \frac{X}{K}\right) - c\frac{X^p}{X^p+H^p}$	K (carrying capacity) $= 10$; $p = 2$; c (maximum grazing rate; control parameter: 1–3)	Grazing on a population (X) that grows logistically; May 1977
$\frac{dX}{dt} = a - bX + c\frac{X^p}{X^p+1}$	a (nutrient load; control parameter: .1–.6); c (maximum recycling rate) $= 1$; $p = 8$; $H = 1$; decay rate $b = .8$	Nondimensional version of a model of nutrient (X) cycling in lakes; Carpenter et al. 1999
$\frac{dE}{dt} = r_E E\left(1 - \frac{E}{E_0}\frac{h_V+V}{h_V}\right)$ $\frac{dV}{dt} = r_V V\left(1 - V\frac{h_E^p+E^p}{h_E^p}\right)$	E_0 (control parameter: 1–10 m^{-1}); growth rates $r_E = .1$; $r_V = .05$ day^{-1}; critical macrophyte cover $h_V = .2$; critical light attenuation to get vegetation $h_E = 2$ m^{-1}; $p = 4$	Macrophyte cover (V) and vertical light attenuation (E) in lakes; Scheffer 1998; van Nes and Scheffer 2005
$\frac{dN_1}{dt} = \frac{r_1 N_1(K_1 - N_1 - \alpha_{1,2}N_2)}{K_1}$ $\frac{dN_2}{dt} = \frac{r_1 N_2(K_2 - N_2 - \alpha_{2,1}N_1)}{K_2}$	Growth rate $r_1 = r_2 = 1$ day^{-1}; carrying capacity K_1 (control parameter: 1–10); $K_2 = 1$ g m^{-2}; competition coefficients $\alpha_{1,2} = 1.4$, $\alpha_{2,1} = 1.2$	Two-species (N_1, N_2) Lotka-Volterra competition model; Lotka (1925) 1956; Edelstein-Keshet 1988
$\frac{dN_i}{dt} = \frac{r_i N_i(K_i^* - \sum_j \alpha_{i,j}N_j)}{K_i^* + u}$ $K_i^* = K_i(1 + M\eta_i)$	$i = 1, 2, \ldots, n$; $\alpha_{i,i} = 1$; $\alpha_{i,j} =$ randomly drawn competition coefficients; $N_i =$ species i; M (control parameter) $=$ environmental factor that affects the carrying capacities K_i; $\eta_i =$ sensitivity coefficient of each species to M; $u =$ small immigration factor to prevent unrealistically low species biomasses; $n = 20$ species	Multispecies (N_i) Lotka-Volterra competition model with external forcing; van Nes and Scheffer 2004

Note: For the description and parameters of the individual-based model, see van Nes et al. 2002.

domly drawn competition coefficients that was used before to show that such model can have alternative stable states.

The last model is a relatively realistic individual-based model describing the dynamics of submerged macrophytes in a lake (van Nes et al. 2003). We used the parameter settings that van Nes et al. (2002) used to describe the dynamics of *Chara aspera* in Lake Veluwemeer.

These models cover various degrees of complexity (the last two are complex). They also represent mathematically different kinds of catastrophic thresholds (see appendix in the online edition of the *American Naturalist*).

Methods

Measuring Recovery Rate after Perturbation

Recovery rates are inferred from the amount of time that the system needs to reach equilibrium after a small disturbance. A commonly used approach to determine this stability measure is to use an asymptotic approximation, that is, the recovery rate to equilibrium after an infinitesimal disturbance (e.g., Beddington et al. 1976; DeAngelis 1980; Neubert and Caswell 1997). In a model, this recovery rate can be determined by linearizing in the stable equilibrium and determining the eigenvalues. The dominant (i.e., maximum) real eigenvalue is an approximation of the recovery rate to equilibrium (Beddington et al. 1976; DeAngelis 1980; Pimm 1984), even though for complex systems it might neglect some transient behavior (Neubert and Caswell 1997). We followed this approach to estimate

recovery rates by linearizing the models and determining the maximal real part of the eigenvalues of the numerically approximated Jacobian matrix (using "Grind" for MATLAB; see http://www.dow.wau.nl/aew/grind/).

For the individual-based model of aquatic macrophytes (van Nes et al. 2002), the eigenvalues cannot be computed in the same way as for the differential equation models. The problem is that the initial state cannot be defined in a simple way because individuals have different properties simultaneously. Furthermore, the seasonal reproduction cycle is a complicating factor. Therefore, in this case, we estimated the recovery rates in the year-to-year biomass by the following numerical procedure. The control parameter (vertical light attenuation without vegetation effect, which can be interpreted as nutrients) was changed in 80 small steps. After each step, the model was stabilized for 50 years; thereafter, the vertical light attenuation was decreased during 1 year by 0.5 m^{-1}. After this disturbance, the model was run for 200 years to let it fully recover. The average of the summer biomass of the last 50 years was used as an estimation of the equilibrium biomass. The last 5 years in which the vegetation biomass differed from this equilibrium by more than an arbitrary small fraction (0.01%) were used to find the recovery rate, assuming exponential decay for the biomass deviation from the equilibrium by linear regression of log-transformed data.

Measuring Ecological Resilience

Ecological resilience, defined as the maximum disturbance a system can take without shifting to an alternative state

(Holling 1973), is not so easily quantified, even in models. An ambiguity is that it is not obvious whether the disturbance should be in the state space (e.g., an instant mortality event) or one should also consider disturbances in parameters (e.g., a temperature peak). Furthermore, determining the maximum possible disturbance in the state space is not easy in individual-based models and complex models with many state variables because in such models a disturbance can be defined in many different ways. To avoid these problems, we simply take the distance in a control parameter (e.g., nutrient loading) to the catastrophic threshold value as a measure of ecological resilience for all models. This is a measure of how much that parameter would need to be perturbed to reach the threshold point, and it correlates to the size of the basin of attraction.

Simulated Pulse Perturbation Experiment

One may think of a pulse perturbation experiment (Bender et al. 1984) to measure recovery rate in practice. In contrast with the proposed experiments of Petraitis and Dudgeon (2004), the perturbation we have in mind here should be rather small because it is not the intention to induce a regime shift. The only requirement is that the perturbation is large enough to be distinguished from the normal fluctuations in the system. If, after the perturbation, the recovery is monitored, an exponential model can be fitted to the time series:

$$\frac{dx}{dt} = -\lambda(x - \mu), \tag{1}$$

in which x is the state variable (e.g., biomass) and μ is the equilibrium biomass; λ is the recovery rate. Both μ and λ can be fitted using standard procedures. Alternatively, the above model can be solved as

$$x_t = \mu + \delta e^{-\lambda t}, \tag{2}$$

in which the model is initially disturbed by $\mu + \delta$. We tested this method with a computer experiment. We added red noise to the May (1977) model. This was done by replacing the parameter c (grazing rate) with a time series generated by a simple recurrence equation for red noise (Hasselmann 1976):

$$c_t = \left(1 - \frac{1}{P}\right)(c_{t-1} - c_O) + c_O + \beta\varepsilon, \tag{3}$$

where P is a parameter that expresses the approximate period of the noise in days (or other time units; $P >$

$1 =$ red noise), c_0 is the approximate mean of the grazing rate, β is parameter that expresses the daily deviation, and ε is drawn daily from a standard normal distribution. Our perturbation was a reduction of the biomass X by 10%. The generated time series was sampled every second day, and μ and λ in equation (1) were fitted using a simplex procedure (as implemented in MATLAB).

Results

In all the simple models we analyzed, the recovery rate shows an almost linear relationship to ecological resilience close to the threshold point, while in most cases farther away from this point, the increase of recovery rate with ecological resilience levels off (fig. 2; fig. A2 in the online edition of the *American Naturalist*). This pattern implies that close to a catastrophic shift (where the basin of attraction shrinks to nil), the recovery rate to equilibrium after a disturbance slows to zero. Farther away from the catastrophic shift, this relation is usually weaker (especially in the Carpenter model; fig. 2b), though this is dependent on the chosen parameters and control parameters (not shown).

In the complex individual-based and multi-species competition models, the estimated recovery rates also drop as the threshold is approached (fig. 3). The irregularity in the relation of the individual-based model (fig. 3d) is probably due to stochasticity related to mortality and possibly rounding-off errors in the model, as we are calculating differences between years. Both cause small irregularities between subsequent years. Although one could consider this a model artifact, it also indicates that in practice it may be difficult to detect differences in ecological resilience in a very precise way.

Our results suggest that critical slowing down is not something that arises only if the system is already very close to a threshold point. In most of the models we tested, the recovery rates change with ecological resilience, even far from the critical point. For instance, figure 2 shows monotonically increasing relationships between recovery rates and ecological resilience over the entire parameter ranges where the models have alternative stable states. Similarly, for the two more complex models, the analysis (fig. 3) shows that the drop in recovery rates already starts far away from the threshold when the ecological resilience is still high. This is important, as it suggests that recovery rates may often serve to signal changes in ecological resilience even if the system is still relatively far from a critical threshold. Our simulated pulse perturbation experiment (see "Methods") exemplifies that a drop in return rates may indeed be measured in noisy time series from a system approaching a critical threshold (fig. 4).
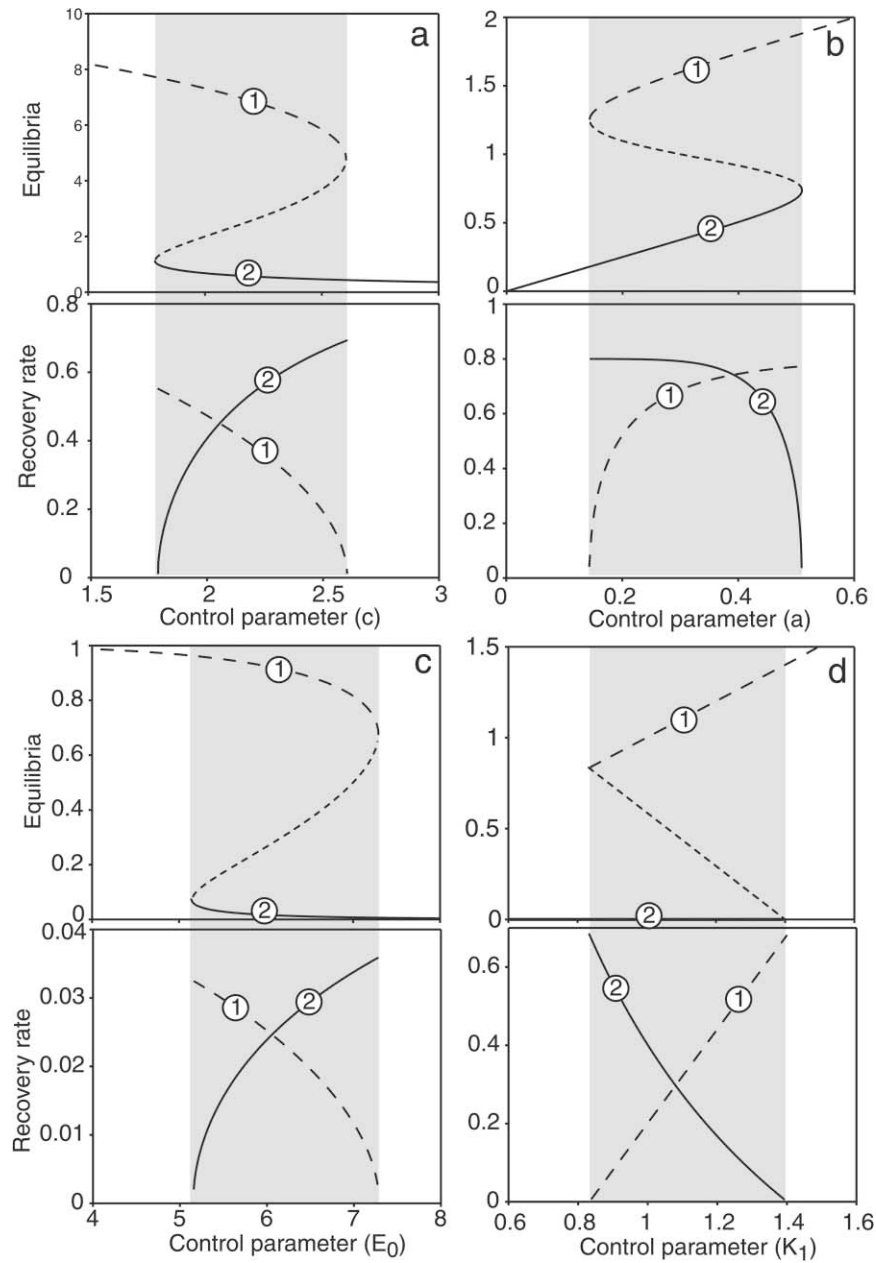
Figure 2: Graphs showing how recovery rate (per day) from small perturbations changes as a catastrophic bifurcation is approached for four models: *a*, grazing on a population that is logistically growing (May 1977); *b*, nutrient cycling in lakes (Carpenter et al. 1999); *c*, macrophytes (*V*) and vertical light attenuation (*E*) in lakes; and *d*, two species Lotka-Volterra. The upper graph of each pair shows the catastrophe fold in the equilibria of the model in response to a control parameter (inflection points at the border of the shaded area are the bifurcation points). The lower graphs show the recovery rates (determined from the eigenvalues; see text) from small perturbations from each of the two stable branches of the catastrophe fold. For clarity, the upper branch of the catastrophe fold and the corresponding recovery rate curve are shown as long dashed lines (and labeled *1*), whereas the lower equilibrium branch and its corresponding recovery rate curve are solid (labeled *2*). The short dashed lines represent the unstable saddle/node that separates the basins of attraction. In models with more state variables, results are shown for one of the variables only (vegetation cover in *c* and biomass of species 1 in *d*). For parameters, see table 1.
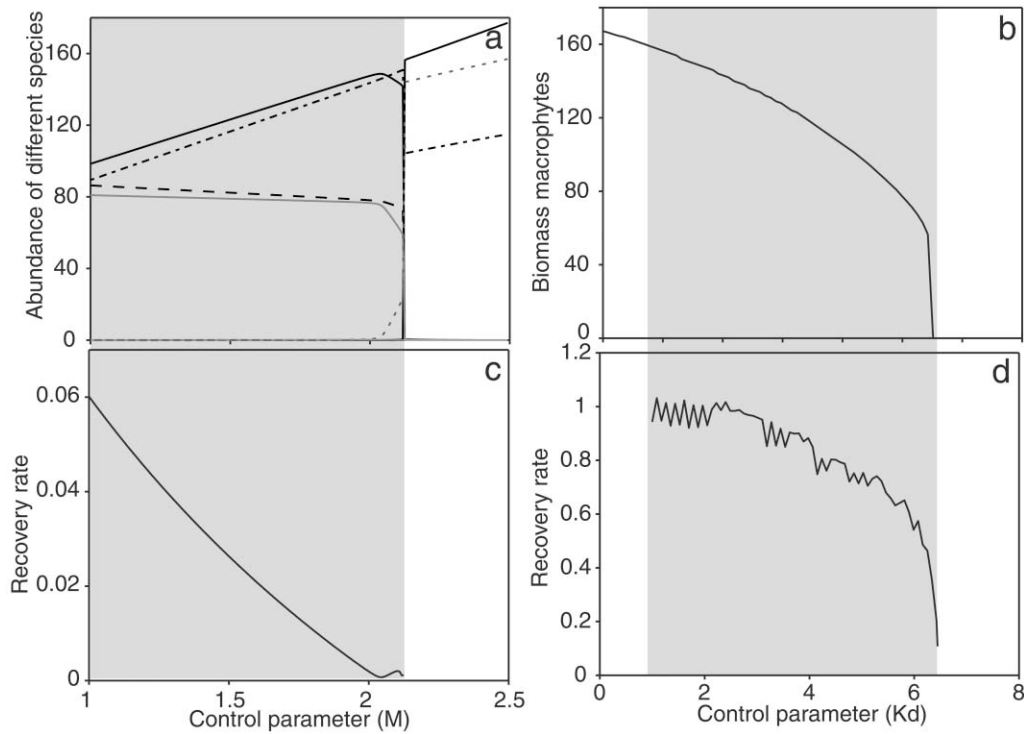
Figure 3: Relation between distance to threshold in control parameter and the recovery rate after a small disturbance for the two more complex models (*c, d*). *a* and *b* indicate the biomasses of species as a function of a very slowly increasing control parameter. The left-hand graphs are from the multispecies Lotka-Volterra model, and the right-hand graphs are from the individual-based model of lake vegetation (a 10 × 10 grid with 1-m depth; parameters as in van Nes et al. 2002).

Discussion

It can be proved that for all continuous differential equations, recovery rates after small perturbations will decrease close to a catastrophic threshold (Wissel 1984). This phenomenon is known in physics as "critical slowing down." In the appendix, we give an intuitive explanation of the phenomenon. Interestingly, the two other known generic indicators (increased variance and red shift in the frequency spectrum) can be at least partly explained by critical slowing down (Ives et al. 2003; Kleinen et al. 2003; Brock and Carpenter 2006; Carpenter and Brock 2006). Though the mathematical generality of critical slowing down is promising, it does not guarantee that it is useful as an indicator in practice. In the next section, we will discuss various practical questions in relation to the potential use of the indicator.

The Possibility of False Positives

It is important to note that critical slowing down can theoretically lead to false positives because it does not necessarily indicate a switch to an alternative state (see appendix). It will, for instance, also occur if a predator-prey system becomes cyclic. It can even happen if a threshold is approached that merely implies an increased sensitivity of the system (fig. 5*c*). With respect to the latter point, it may seem disappointing that a drop in recovery rates may indicate either an upcoming catastrophic shift to an alternative basin of attraction or a "mere" high sensitivity of the system around a critical condition. However, those two situations are in fact closely related and may often arise in the same kind of system. Depending on the conditions, there may or may not be alternative stable states when changing a control parameter. For example, macrophyte abundance may respond catastrophically to increasing nutrient loading if they are in shallow lakes and smoothly if they are in deeper systems.

For a range of systems (e.g., shallow lakes or the thermohaline circulation), we have a priori reasons to expect that a catastrophic threshold must exist. The challenge then is to know whether we are getting close to the threshold. It is in those situations that indicators such as recovery rates are perhaps most interesting to study.
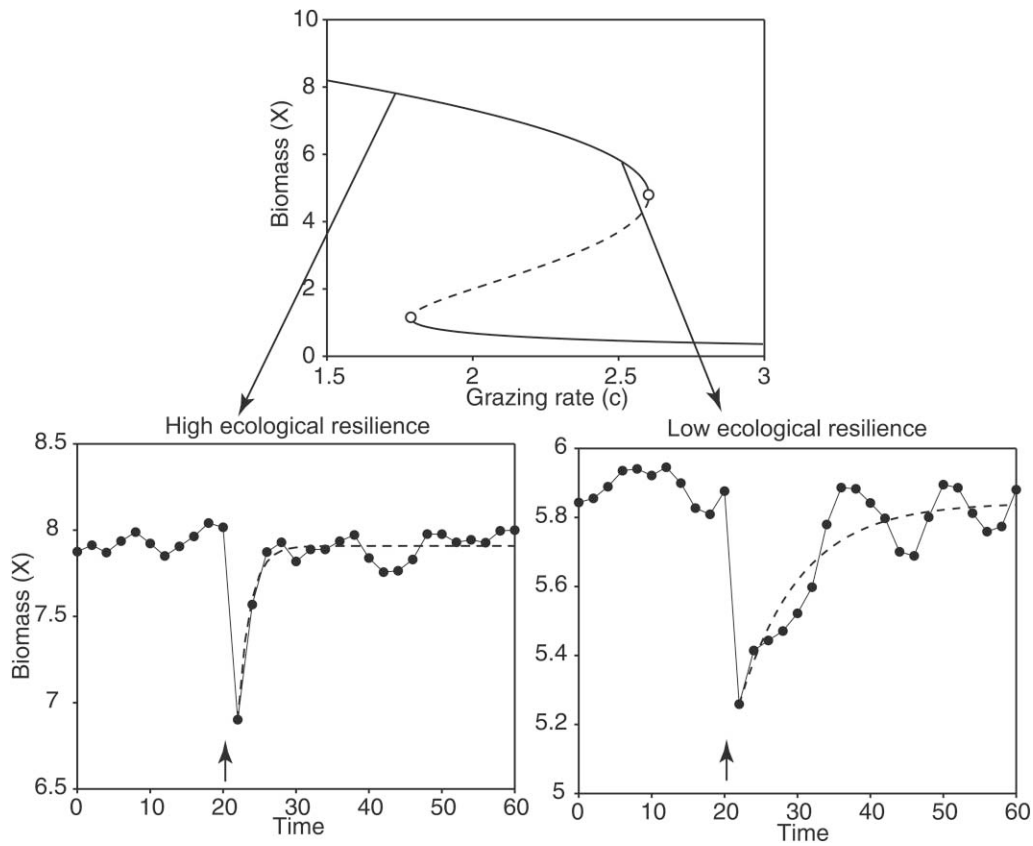
Figure 4: Simulated pulse perturbation experiments using the May (1977) model with red noise on parameter *c* (noise normally distributed with *P* of 5 days and *β* of 0.1). Difference in recovery rates is obvious when comparing a situation far from a bifurcation (*lower left*; *c* = 1.7) and a situation close to a bifurcation (*lower right*; *c* = 2.5). In both cases the perturbation consists of a 10% reduction in biomass (*vertical arrows*). The recovery time is determined by fitting an exponential decay (λ = 0.12 and 0.6, respectively), using a simplex method (see "Methods").

How Early May the Early Warning Signal Be Detected?

Our analysis suggests that critical slowing down usually occurs far enough from the critical threshold to be usable as early warning signal. In all the models we tested (except perhaps Carpenter's model), ecological resilience was positively, and often almost linearly, related to recovery rate over a large domain of the control parameter. However, this is not necessarily a generic feature. For instance, Nakajima and DeAngelis (1989) showed that slowing down of recovery rates can occur only very close to a threshold (here a Hopf bifurcation, where the system becomes cyclic).

Interpreting Change in Recovery Rate Rather than Absolute Values

Although the decrease of recovery rate close to a threshold is generic, the slope of the relationship between recovery rate and the width of the basin of attraction will be specific to any particular system. It depends simply on the typical timescales of change in the system (e.g., the slowest reproduction rate of key species). Thus, absolute values of recovery rates are not very informative by themselves when it comes to signaling the proximity of a catastrophic threshold. Instead, we need to consider relative differences. For instance, it makes little sense to try to interpret differences in recovery rates between a forest and a plankton system in terms of their vicinity to a threshold. Plankton recovery rates will always be faster, even if the planktonic system is close to a critical threshold. By contrast, if we want to compare, for instance, the width of the basin of attraction of two clear shallow lakes or to monitor ecological resilience of a lake as nutrient loading increases, differences in recovery rate after small perturbations are likely to be meaningful.

Recovery from Small versus Large Perturbations

Our analysis relates to recovery rates from very small perturbations around the equilibrium. However, our simu-
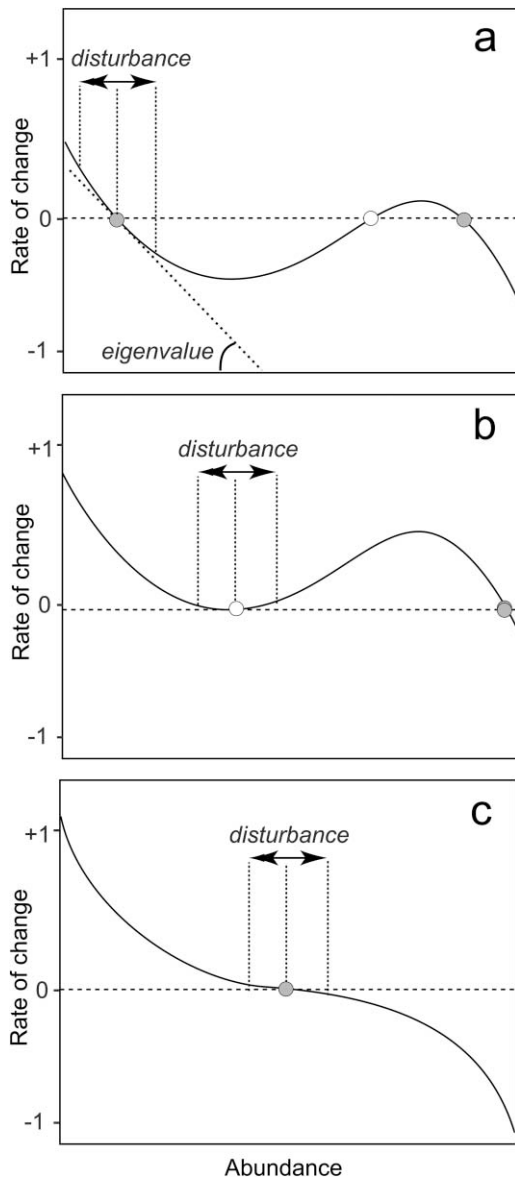
Figure 5: Rate of change as a function of abundance for a hypothetical population with alternative equilibria (*gray circles*). The unstable equilibrium (*open circle*) represents the border of the basins of attraction of the two stable points (*a*). In the threshold point (*b*), the stable and unstable equilibria merge, and the slope of the function that describes the relationship between the rate of change and the population density becomes zero. As one gets farther away from the bifurcation (*a*), this slope (i.e., the eigenvalue) becomes larger. This implies that the rate of recovery from a small perturbation decreases as the system approaches the bifurcation. If the rate of change decreases with abundance over the entire parameter range (*c*), the model cannot have alternative equilibria. However, in the illustrated case, the state changes relatively steeply around a threshold value, and here the rates of change are again small near the equilibrium. This implies that critical slowing down will also mark such noncatastrophic thresholds.

lated experiment indicates that slowing down is not restricted to very small perturbations. Obviously, recovery from larger perturbations may also be delayed if they bring the system close to the unstable equilibrium that represents the tipping point. However, this is a quite different phenomenon. Clearly, it is less useful as a way to probe resilience, since such large perturbations would also imply a large risk of inducing a large-scale catastrophic shift. Therefore, it is interesting that, perhaps unexpectedly, even the response to relatively small perturbations that do not bring the system into the vicinity of a tipping point may still reflect ecological resilience (figs. 2, 3).

Estimating Recovery Rates from Experimental Data

Measuring recovery rates in real ecosystems is not an easy task in practice. Our simulated pulse experiment (fig. 4) looks promising. However, the perturbation should be larger than natural variation, implying that the method may be difficult to apply in systems with a large natural variation. Note that in spatially heterogeneous ecosystems, one might experimentally perturb the system locally and measure the rate at which the experimental patch returns to equilibrium. For instance, we could clear out a small patch of aquatic vegetation and measure the recovery rate. This is attractive from a practical point of view. However, one should keep in mind that spatial heterogeneity, irregular movement of key species (Nyström and Folke 2001), and the spatial scale of the disturbance (Petraitis and Latham 1999) may affect the results.

Estimating Recovery Rates from Natural Time Series

Although experimental perturbation seems a promising way to probe differences in ecological resilience, it does not help to estimate resilience of natural systems in hindsight. However, there are ways to use natural time series to infer ecological resilience too. For instance, we might attempt to use, as a surrogate for experimental perturbations, information about the response of a system to stochastic natural disturbances. Held and Kleinen (2004) propose a way of inferring recovery rates to equilibrium from time series analysis. They suggest that if a time series with a fixed small time step of sampling Δt is available, it should be possible in principle to use these data to fit an autoregressive model ($y_{n+1} = \exp\left[-\lambda\Delta t\right]y_n + \sigma\varepsilon_n$, where y_n is the deviation of a measurement from the equilibrium at time n, ε_n is Gaussian white noise, and the recovery rate λ and the intensity of the noise σ are parameters to be fitted). For more statistical and methodological details about these techniques, we refer to Ives (1995) and Ives et al. (2003). This so-called degenerate fingerprinting technique indeed seems an interesting possibility despite being

data demanding and although frequently measured equidistant time series are rare in ecology.

In conclusion, although we are still at the first stages of exploring the use of slowing down of recovery as a signal of upcoming catastrophic shifts, our first results are promising. Many of the drawbacks of critical slowing down that we discussed are shared with the other generic indicators (Kleinen et al. 2003; Carpenter and Brock 2006). They are all relative measures, data demanding, and unlikely to work in systems with large variation. Nonetheless, since prediction of regime shifts in other ways is notoriously difficult, we have no other options. Therefore, it seems worthwhile exploring the practical use of these and other potential early warning signals further.

Acknowledgments

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