



Ecosystems off track: rate-induced critical transitions in ecological models

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Theory suggests that gradual environmental change may erode the resilience of ecosystems and increase their susceptibility to critical transitions. This notion has received a lot of attention in ecology in recent decades. An important question receiving far less attention is whether ecosystems can cope with the rapid environmental changes currently imposed. The importance of this question was recently highlighted by model studies showing that elevated rates of change may trigger critical transitions, whereas slow environmental change would not. This paper aims to provide a mechanistic understanding of these rate-induced critical transitions to facilitate identification of rate sensitive ecosystems. Analysis of rate sensitive ecological models is challenging, but we demonstrate how rate-induced transitions in an elementary model can still be understood. Our analyses reveal that rate-induced transitions 1) occur if the rate of environmental change is high compared to the response rate of ecosystems, 2) are driven by rates, rather than magnitudes, of change and 3) occur once a critical rate of change is exceeded. Disentangling rate-induced transitions from classical transitions in observations would be challenging. However, common features of rate-sensitive models suggest that ecosystems with coupled fast–slow dynamics, exhibiting repetitive catastrophic shifts or displaying periodic spatial patterns are more likely to be rate sensitive. Our findings are supported by experimental studies showing rate-dependent outcomes. Rate sensitivity of models suggests that the common definition of ecological resilience is not suitable for a subset of real ecosystems and that formulating limits to magnitudes of change may not always safeguard against ecosystem degradation.

Synthesis

Understanding and predicting ecosystem response to environmental change is one of the key challenges in ecology. Model studies have suggested that slow, gradual environmental change beyond some critical threshold can trigger so-called critical transitions and abrupt ecosystem degradation. An important question remains however whether ecosystems can cope with the ongoing rapid anthropogenic environmental changes to which they are currently imposed. In this study we demonstrate that in some ecological models elevated rates of change can trigger critical transitions even if slow environmental change of the same magnitude would not. Such rate-induced critical transitions in models suggest that concepts like resilience and planetary boundaries may not always be sufficient to explain and prevent ecosystem degradation.

Theoretical studies have suggested that gradual changes in environmental conditions may trigger so-called critical transitions in ecosystems, which would explain unexpected ecosystem degradation and the sudden emergence of cyclic or chaotic dynamics (Holling 1973, Scheffer et al. 2001, Scheffer 2009). These studies found that gradual external change can undermine the resilience of ecosystems, thereby increasing their susceptibility to critical transitions. The resilience of ecosystems can be assessed with ecological models through steady state analysis. Steady state analysis allows determining critical magnitudes of change in external conditions and critical levels of disturbance beyond which ecosystems shift to alternative dynamics. The assumption behind steady state analysis is that an ecosystem is in a state in which all processes balance out and no change can be observed (i.e. in dynamic equilibrium). Although

the assumption that ecosystems reside in such a steady state has been useful in assessing their resilience under static or slowly changing environmental conditions, it does not hold when changes in environmental conditions are rapid relative to the attractive capacity of a steady state. The fact rapid environmental changes may lead to unexpected ecosystem dynamics has received only little attention in the ecological community (Scheffer et al. 2008). This is remarkable as the environmental changes in the Anthropocene occur at unprecedented rates (Joos and Spahni 2008, Kaplan et al. 2011, Klein Goldewijk et al. 2011) and may be too rapid for ecosystems to cope with (Walther et al. 2002). In this study, we show that models indeed suggest that some ecosystems may fail to respond to rapidly changing external conditions, which can lead to a novel type of critical transition. We identify mechanisms driving such rate-induced

critical transitions, provide possible ways forward regarding identification of rate sensitive ecosystems and discuss the implications of rate-induced critical transitions for the general view on ecological resilience.

Critical transitions, steady state analysis and resilience

A critical transition is a shift of a system to a qualitatively different dynamical regime triggered by changing external conditions or by a disturbance. Critical transitions can be super- or subcritical. Supercritical transitions are continuous and reversible whereas subcritical transitions are discontinuous and require disproportional efforts to reverse. Subcritical transitions that occur between steady ecosystem states are also referred to as catastrophic shifts (Scheffer et al. 2001). Well-known examples of catastrophic shifts are transitions of shallow lakes from clear to turbid states, triggered by increases in nutrient input (Scheffer et al. 1993), of grazing systems from vegetated to (bare) overgrazed states forced by an increase in herbivore density (Noy-Meir 1975, May 1977, Rietkerk et al. 1996, 1997) and of marine ecosystems driven by (combinations of) sea temperature rise, overfishing, habitat loss, invasive species and pollutants (Jackson et al. 2001, Petraitis 2013). The alternative dynamics to which a system transitions do not necessarily have to be steady over time. Increases in primary production through nutrient enrichment, for example, are known to lead to cyclic dynamics between predators and preys (Huffaker et al. 1963, Rosenzweig 1971). In addition to these predator–prey cycles more discrete repetitive catastrophic shifts can occur in ecosystems with coupled fast–slow dynamics (Rinaldi and Scheffer 2000). Examples of such ecosystems are the spruce–budworm ecosystem, in which the recovery of trees from defoliation occurs at a much slower rate than the budworm outbreaks (Ludwig et al. 1978, Holling 1988) and coastal dune ecosystems in which repetitive shifts between wet and dry soils are thought to occur due to soil water repellency, thereby controlling the much slower vegetation dynamics (Siteur et al. 2016).

Besides cyclic and static dynamics, ecosystems may transition to apparently random dynamics when environmental conditions change. Such chaotic dynamics are solely caused by deterministic processes and can even occur if the mechanisms controlling the system are very simple and are ought to result in trivial behaviour (May 1976, Tilman and Wedin 1991). In addition to transitions towards alternative temporal dynamics, spatially extended ecosystems can change their spatial structure in response to environmental changes. In arid ecosystems for example, declining rainfall may trigger the formation of spatially periodic patterns in vegetation (Klausmeier 1999, Valentin et al. 1999, Von Hardenberg et al. 2001, Rietkerk et al. 2002).

The notion that environmental change may trigger non-linear ecosystem response can largely be attributed to modelling efforts in the second part of the 20th century. In the field of mathematics, the description of natural phenomena using difference and differential equations is referred to as dynamical systems theory, which was introduced by Sir Isaac Newton back in the 17th century to lie the foundations of what is now known as classical mechanics (Newton 1687) and which was later further developed by Henri Poincaré (Poincaré and Magini 1899). Although

the term ecosystem had already been coined in the 1930s (Tansley 1935, Willis 1997) and population models had been used well before that (Pisano 1202, Verhulst 1838, Volterra 1928), the dynamical systems approach only got widely applied in ecology in the 1970s (Rosenzweig 1971, Noy-Meir 1975, May 1977).

The application of the dynamical systems approach to ecology was aided by graphical approaches that enabled analysis of ecological models (Rosenzweig and MacArthur 1963). However, the rapid development of theoretical ecology was also closely related to advancements in the mathematical field of bifurcation theory, or more specifically catastrophe theory. Catastrophe theory, from which the term catastrophic shift is derived, was introduced by René Thom (Thom 1975) and further developed by Christopher Zeeman (Zeeman 1976, Zeeman and Barrett 1979). It applies topology to families of fixed points (or steady states/equilibria) to obtain a set of elementary phenomenological models that show how “continuous causes can give rise to discontinuous effects” (Zeeman 1982). One of the elementary models describes the so-called fold catastrophe. Equation 1 is one way this elementary model can be formulated (modified from Ashwin et al. 2012) and describes the dynamics of state variable x as function of itself and two parameters a and b :

$$\frac{dx}{dt} = b - (x - a)^2 \quad (1)$$

Figure 1a shows that a gradual decline in parameter b initially results in a minor response of state variable x . However, if parameter b decreases beyond a critical threshold value then a catastrophic shift occurs.

This behaviour, as well as that of many ecological models, can very well be understood by applying a steady state approximation. As noted above, this approximation enables the derivation of steady states (i.e. dynamic equilibria). Over time, the actual state of a system will move to a steady state if it is stable, and will move away from it when unstable. If a stable steady state only attracts within a certain “basin of attraction” (Lewontin 1969), it is said to be locally stable (as opposed to globally stable). The proximity of the system state to the boundaries of the basin of attraction and the change in parameters required to pass critical thresholds (i.e. the persistence of the basin of attraction) determines the resilience of an ecosystem. Thus, ecological resilience can be defined as a measure of the ability of ecosystems to absorb changes of state variables, driving variables, and parameters, and still persist (Holling 1973).

Figure 1 shows that, as parameter b declines, the system closely follows a stable steady state (Fig. 1a) until the basin of attraction vanishes (Fig. 1b). Steady state analysis allows deriving the critical threshold value of b at which the basin of attraction vanishes, as well as the boundary of the basin of attraction, here given by the unstable steady state (Supplementary material Appendix A). Given the external conditions and the state of the system, this allows deriving the critical magnitude of change in b and the critical perturbation size in terms of x , beyond which the system shifts to alternative dynamics as depicted in Fig. 1a. These properties directly relate to the definition of ecological resilience (Holling 1973). The susceptibility of ecosystems to the types of critical transitions described so far can thus be assessed and understood through steady state analysis of ecological models.

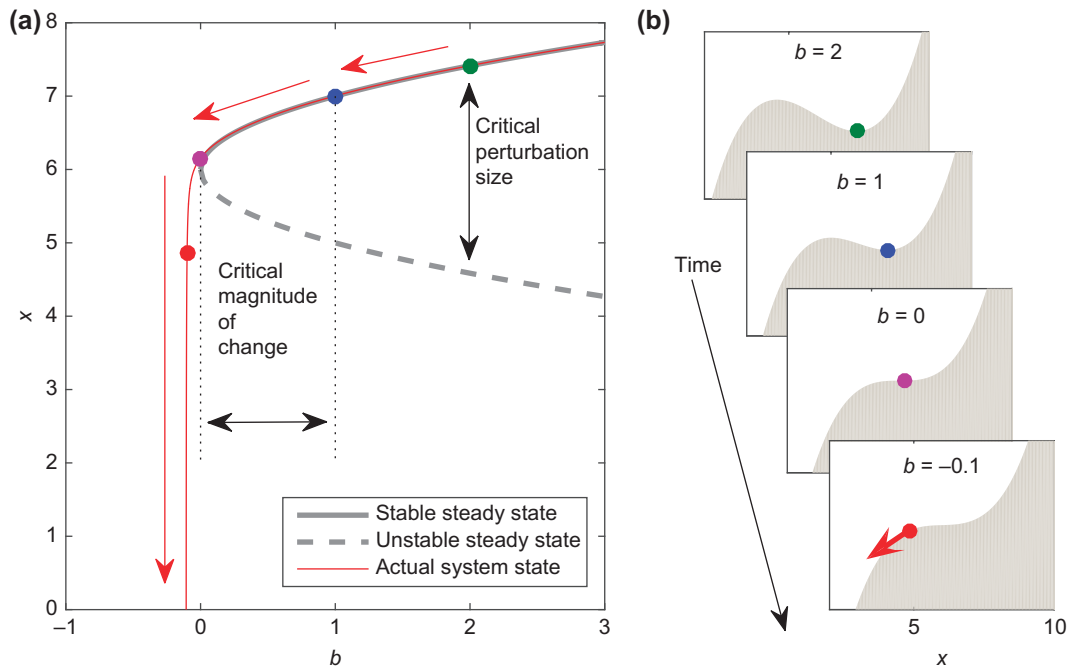


Figure 1. (a) Critical transition in a fold catastrophe model (Eq. 1) triggered by a gradual decrease in parameter b ($db/dt = -0.1$ and $a = 6$). (b) Potential landscapes for different values of b , showing the vanishing of the basin of attraction as b declines. The coloured dots depict the system state at $b = 2$ (green), $b = 1$ (blue), $b = 0$ (pink) and $b = -0.1$ (red). In (a) the gray lines give the stable (solid) and unstable (dashed) steady states of the system (i.e. assuming $db/dt = 0$). See Supplementary material Appendix A for a derivation of the steady states and potential diagrams.

Rate-induced critical transitions

As illustrated in Fig. 1b, steady state analysis can often properly explain the complex dynamics exhibited by ecological models. However, one can question the validity of the steady state assumption if external conditions change more rapidly. From a mathematical perspective, models with explicit time dependency of one of the parameters (also referred to as non-autonomous, open or ramped systems; Wicczorek et al. 2010, Ashwin et al. 2012) do generally not have steady states. In analysis of ecological models it is therefore often implicitly assumed that external conditions change slowly compared to the attractive capacity of an ecosystem's stable steady state, such that it approximates the actual system state. While this may be true for ecosystems that are relatively isolated from human activities, the currently observed rates of anthropogenic environmental change could be much higher than the rate at which ecosystems can respond to these changes (Walther et al. 2002). This could result in dynamics that differ from the dynamics predicted by steady state analyses and may even trigger unexpected critical transitions. This would have consequences, not only for the validity of currently applied model analyses, but also for our view on ecological resilience (e.g. as defined by Holling 1973).

Runs of the model described by Eq. 1 suggest that if external conditions change rapidly, the actual system state can indeed strongly deviate from the stable steady state, as shown in Fig. 2a. For relatively slow external changes, now simulated by increasing the value of parameter a , the actual system state simply lags behind the stable steady state. However, above some critical rate of change in a , the system is unable to cope with the rapid changes. The rapid increase in a then drives the system state out of the basin of attraction (Fig. 2b) and away from the stable steady state. Notice that in this example the

two classical measures for resilience identified in the previous section, i.e. the width and the persistence of a basin of attraction (Fig. 1a), are not affected by changes in a . Yet, high rates of change in a can still trigger a critical transition.

The critical transition shown in Fig. 1 occurs once a critical magnitude of change is exceeded, which can be derived by calculating the distance to the critical threshold value of b . In contrast, the transition depicted in Fig. 2 occurs when external conditions (parameter a) change with a rate that exceeds a certain critical rate of change. To distinguish between the two types of transitions we will refer to them with the terms 'change-induced critical transition' and 'rate-induced critical transition' respectively. Systems that are able and likely to display rate-induced critical transitions will be referred to as 'rate sensitive systems'.

Although it is quite intuitive that some ecosystems may not be able to respond timely to rapidly changing conditions, this concept has only recently received attention in theoretical ecology (Scheffer et al. 2008). In the field of neuroscience, however, rate sensitivity of neural cells is a well-known phenomenon. Neural cells are excitable, that is, if an electric current is passed through neural cell tissue excitation can occur, driving further transmission of the current. Excitation only occurs if the current exceeds a certain threshold value. However, accommodation occurs in response to the current, meaning that the critical threshold rises over time (Hill 1936). As a result, excitation is rate dependent. A model that reproduces these dynamics is a modification of the Van der Pol oscillator (Van der Pol 1920, FitzHugh 1961) and shows that excitation can occur if sufficiently large "cathodal shock" is applied (FitzHugh 1961).

More recently, rate-induced critical transitions have received considerable attention in the mathematical literature

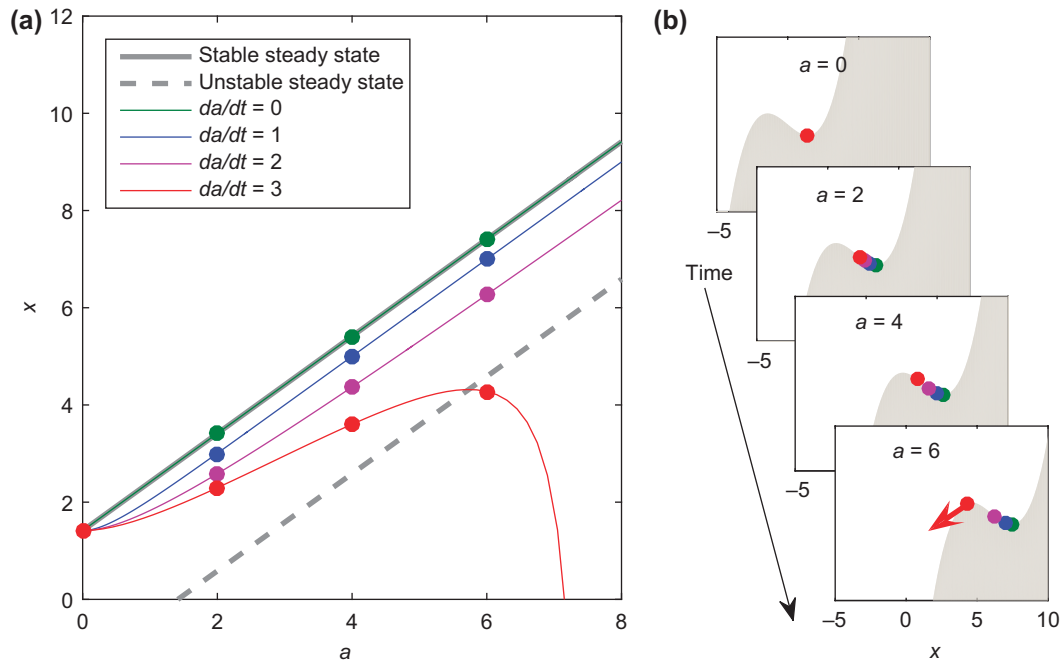


Figure 2. (a) Rate-induced critical transition in a fold catastrophe model (Eq. 1) triggered by a rapid increase in a . Increases in a can trigger a critical transition, provided that the rate of change in a is sufficiently high. (b) The shape of the potential landscape is not affected by a , however rapid changes in a can pull the system out of the basin of attraction. In this figure $b = 2$ and $da/dt = 0-3$. The coloured dots depict the actual system state at $a = 0$, $a = 2$, $a = 4$ and $a = 6$ for different rates of change. In (a) the gray lines give the stable (solid) and unstable (dashed) steady states of the system (i.e. assuming $da/dt = 0$). See Supplementary material Appendix A for a derivation of the steady states and potential diagrams.

(Wieczorek et al. 2010, Ashwin et al. 2012, Perryman 2015). A particularly well studied model is the model by (Luke and Cox 2011). Their model shows that rising atmospheric temperatures may trigger enhanced soil microbial respiration which may further heat soils eventually resulting in a sudden loss of soil carbon and increased CO_2 emissions into the atmosphere. This non-linear response, which they refer to as the ‘compost-bomb instability’, only occurs if atmospheric temperatures rise quickly and is thus rate-induced.

In the ecological literature, a rate-induced critical transition was first described in a model study by Scheffer et al. (2008). In their model, which captures the dynamics of plants and herbivores, plants become less palatable as their biomass increases. An increase in plant productivity results in an increase of herbivore biomass, provided that the productivity rises slowly compared to the response rate of the herbivores. If, on the other hand, productivity rises rapidly, the model shifts from a herbivore controlled state to a plant dominated state without herbivores (Scheffer et al. 2008). In Box 1 we show that rate-induced critical transitions can occur more generally in systems with coupled resource and consumer dynamics.

Analysis of rate sensitive models

As can be deduced from the example shown in the previous section and in Box 1, steady state analysis is insufficient to describe the dynamics of rate sensitive models to rapid changes in parameters as it cannot predict rate-induced critical transitions and therefore may overestimate resilience. Brute force numerical techniques, such as model runs with varying rates of change (e.g. Fig. 2a, Fig. 3b–c and Scheffer

et al. 2008), can be used to study rate sensitivity and to estimate critical rates of change. However, to obtain more general insights into the mechanisms that drive rate-induced transitions and to be able to derive explicit expressions for critical rates of change, analytical techniques are required. Unfortunately, an equivalent to steady state analysis that can be universally applied to study rate sensitive systems has not yet been developed. However, a comprehensive attempt to understand rate sensitivity in models with coupled fast-slow dynamics (such as the model by Rosenzweig and MacArthur 1963 and described in Box 1) was introduced in a paper by Wieczorek et al. (2010). Their approach allows derivation of a critical rate of change through desingularization, time reversal and calculation of eigenvectors. Discussion of this approach goes beyond the scope of this paper, but in the following section we will present two less comprehensive alternative approaches that allow us to analyse the rate-induced critical transition in the model described by Eq. 1. These alternative approaches are introduced here to provide a general mechanistic understanding of rate-induced critical transitions and to enable discussion on the outstanding challenges that come with the analysis of rate sensitive ecological models.

Graphical analysis of Eq. 1

In Fig. 2 we showed that a rate-induced critical transition occurs in the model of Eq. 1 when the actual system state leaves the basin of attraction of the stable steady state, i.e. when it passes the unstable steady state of Eq. 1. This event is triggered by the movement of unstable steady state, which in turn is driven by the change in parameter a . Whether the unstable steady state is able to overtake the actual system

Box 1

An ecological example: rate-induced overconsumption in the Rosenzweig–MacArthur model

An ecological model that can display rate-induced critical transitions is the model by Rosenzweig and MacArthur (1963) with slow consumer dynamics:

$$\frac{dR}{dt} = rR \left(1 - \frac{R}{K} \right) - \frac{aCR}{R + R_h} \quad (2)$$

$$\frac{dC}{dt} = \varepsilon \left(\frac{eaCR}{R + R_h} - mC \right) \quad (3)$$

Here R and C are resource and consumer densities respectively (e.g. in g m^{-2}), r is the resource growth rate (in day^{-1}), K is the carrying capacity (in g m^{-2}), a is the maximum consumption rate (in day^{-1}), R_h is the resource density at which consumption is half this rate (in g m^{-2}), e is an efficiency constant, m is the consumer mortality rate (in day^{-1}) and ε is a small dimensionless parameter that controls the difference in time scales between the fast resource dynamics and the slower consumer dynamics. Notice that what we consider here as consumers and resource is sometimes referred to as exploiter and victim (Rosenzweig 1971), predator and prey (Rosenzweig and MacArthur 1963) or herbivores and plants (Noy-Meir 1975) respectively.

Figure 3 shows how the model responds to declining resource growth rate r . The steady states of the system predict that a change in r affects the consumer density, but not the resource density, as shown in Fig. 3a. Model runs with declining r show something different (Fig. 3b–c). Since the response of consumers is slow, due to the low value of ε , the actual consumer density lags behind its steady state (Fig. 3b). This means that consumption is higher than predicted with steady state analysis, thereby lowering the resource density (Fig. 3c). The response to a slow decline in r is rather linear, since the decrease in consumer density is rapid enough to diminish consumption to a level that enables high resource densities to be maintained. If, however, the rate of change in r is slightly faster, the consumer density does not decline fast enough and overconsumption occurs resulting in sudden depletion of the resource. The rate of the consumer dynamics (controlled by ε), greatly affects the occurrence of rate-induced critical transitions in this model, since the system can tolerate more rapid decreases in r if consumers are able to change their density faster (high ε).

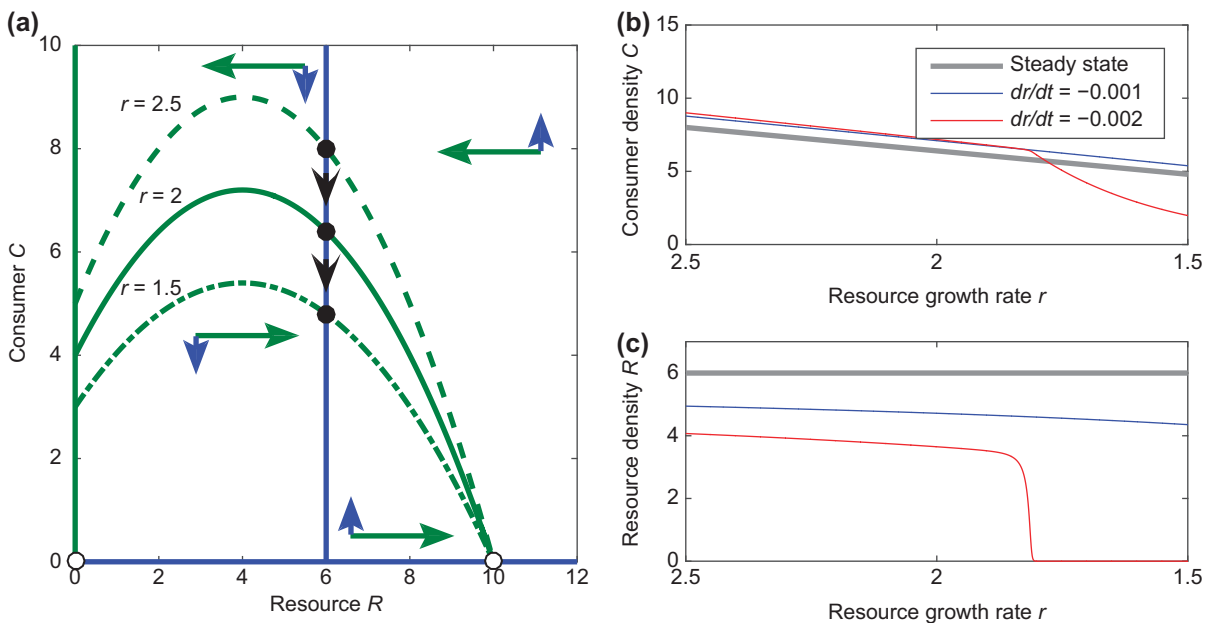


Figure 3. A rate-induced critical transition in the model by Rosenzweig and MacArthur (1963) (Eq. 2 and 3) triggered by a decreasing resource growth rate r . (a) Phase plane of the Rosenzweig–MacArthur model. The green lines are resource isoclines ($dR/dt = 0$) for $r = 2.5$ (dashed), $r = 2$ (solid) and $r = 1.5$ (dash-dotted). The blue lines are consumer isoclines ($dC/dt = 0$). Circles indicate stable (filled) and unstable (open) steady states ($dR/dt = dC/dt = 0$). The black arrows show the movement of the stable steady state as r decreases. The blue and green arrows give the direction of change if the system is not in a steady state. (b, c) Model response to slowly and less slowly declining r . In this figure $r = 1.5$ – 2.5 , $a = 1$, $e = 1$, $K = 10$, $m = 0.75$, $\varepsilon = 0.01$ and $R_h = 2$. The model runs were initiated in the stable steady state of the system at $r = 5$ ($R = 6$, $C = 16$).

state, can be assessed graphically by comparing the maximum response rate of the system under static conditions (i.e. the maximum value of dx/dt) with the movement rate of the unstable steady state, as shown in Fig. 4. This graphical comparison shows that the movement rate of the unstable steady state exceeds the maximum response rate of the system if parameter a changes with a rate beyond a critical rate of change of $da/dt = 2$.

This result can also be obtained analytically by deriving both the maximum response rate and the movement rate of the unstable steady state. The maximum of Eq. 1 is located at $x = a$, meaning that the maximum response rate equals:

$$\frac{dx}{dt} = b - (x - a)^2 = b \quad (4)$$

The unstable steady state is given by $\bar{x}_- = a - \sqrt{b}$ (Supplementary material Appendix A) and its derivative to a equals 1. Thus, the moving rate of the unstable steady state is given by:

$$\frac{d\bar{x}_-}{dt} = \frac{d\bar{x}_-}{da} \frac{da}{dt} = \frac{da}{dt} \quad (5)$$

Equalizing Eq. 4 and 5 yields a critical rate of change in a of:

$$\frac{da}{dt} = b \quad (6)$$

beyond which the unstable steady state is able to overtake the actual system state. Notice that both the graphical and the analytical result correspond with the model runs presented earlier in Fig. 2.

Steady lag analysis of Eq. 1

Figure 2a shows that under steady conditions ($da/dt = 0$) the system can be assumed to reside in a stable steady state $x = \bar{x}_+$, but that as parameter a changes over time ($da/dt \neq 0$) the actual state of the system starts to lag behind its stable steady state. The actual state of the system can then be written as the sum of the stable steady state \bar{x}_+ and the lag of the system state ξ :

$$x = \bar{x}_+ + \xi \quad (7)$$

with $\bar{x}_+ = a + \sqrt{b}$ (Supplementary material Appendix A). Rewriting gives $\xi = x - \bar{x}_+$, so that the change of the lag ξ over time can be written as:

$$\begin{aligned} \frac{d\xi}{dt} &= \frac{d(x - \bar{x}_+)}{dt} \\ &= \frac{dx}{dt} - \frac{d\bar{x}_+}{dt} \\ &= b - (x - a)^2 - \frac{d\bar{x}_+}{da} \frac{da}{dt} \\ &= b - (\bar{x}_+ + \xi - a)^2 - \frac{d(a + \sqrt{b})}{da} \frac{da}{dt} \\ &= b - (a + \sqrt{b} + \xi - a)^2 - \frac{da}{dt} \\ &= b - (\sqrt{b} + \xi)^2 - \frac{da}{dt} \end{aligned} \quad (8)$$

For linear changes in a (i.e. constant da/dt) Eq. 8 becomes autonomous. This means that, unlike Eq. 1, it does not explicitly depend on the changing parameter a . Therefore, we can set $d\xi/dt$ to zero to obtain the steady state of Eq. 8, or the 'stead lag' of x behind the steady state of Eq. 1.

Two steady lags can be found of which $\bar{\xi}_+$ is stable (see Supplementary material Appendix B):

$$\bar{\xi}_{\pm} = \pm \sqrt{b - \frac{da}{dt}} - \sqrt{b} \quad (9)$$

This equation has no solution for $da/dt > b$. Indeed, Fig. 5 shows that, in line with the analysis in the previous section and model runs of Fig. 2a, this model has a critical rate of increase for parameter a of:

$$\frac{da}{dt} = b \quad (10)$$

above which the actual system state is unable to track the stable steady state. Notice that by rewriting in terms of ξ ,

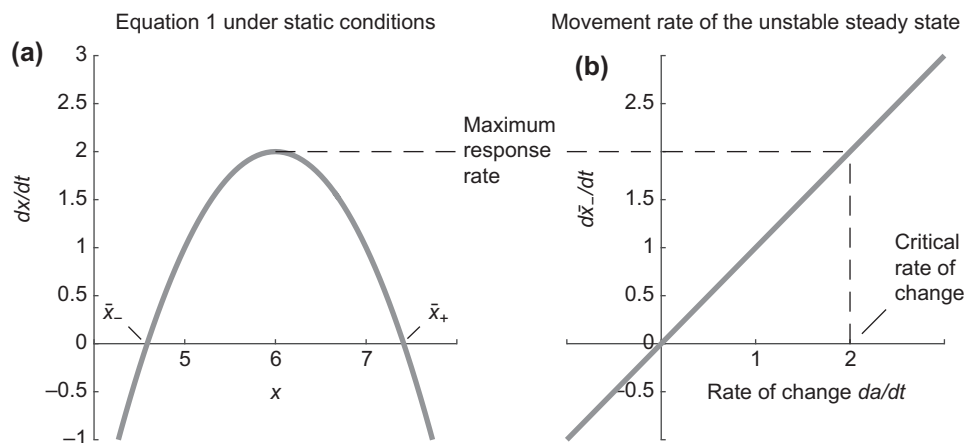


Figure 4. A rate-induced critical transition occurs in the model described by Eq. 1 if the movement rate the unstable steady state exceeds the maximum response rate of the system. (a) Dynamics in x under static conditions, for $a = 6$ and $b = 2$. Here \bar{x}_+ is the stable steady state and \bar{x}_- is unstable steady state, which moves with a rate depicted in (b) as a changes.

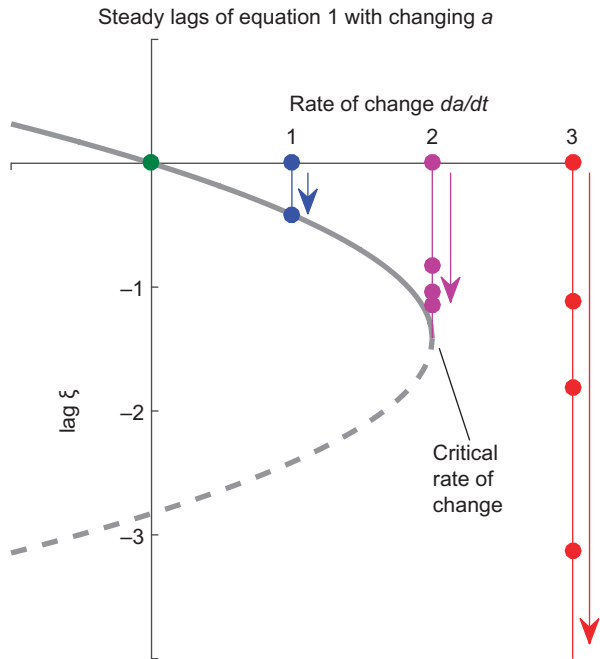


Figure 5. The model described by Eq. 1 lags in a way equivalent to the fold catastrophe model with the rate of change da/dt as driving parameter. The gray solid lines are stable steady lags and the dashed lines are unstable steady lags. The colored lines and dots correspond to the model runs shown in Fig. 2.

the model reduces to the fold catastrophe model with da/dt being the driving parameter.

Understanding rate sensitivity of ecological models

The analyses of Eq. 1 presented above provide a number of key insights regarding the general mechanisms that could be responsible for rate-induced critical transitions in ecological models and real ecosystems. First, the graphical analysis of section ‘Graphical analysis of Eq. 1’ suggests that rate-induced critical transitions are likely to occur when the rate of environmental change is high relative to the maximum response rate of ecosystems (Fig. 4). Second, analysis of the lag of the system state behind its steady state revealed that rate-induced critical transitions are similar to change-induced critical transitions, e.g. they can be described by the fold catastrophe model (Fig. 5), but are driven by rates, rather than magnitudes, of environmental change. Finally, both analyses suggest that rate-induced critical transitions occur once a critical rate of change is exceeded.

Although both analyses provide general mechanistic insights regarding rate sensitivity of models and possibly of real ecosystems, they are only of limited value when studying specific mechanisms that drive rate-induced critical transitions in a particular ecosystem or in more comprehensive ecological models. First, the graphical approach of section ‘Graphical analysis of Eq. 1’ can only be applied to models with one state variable, such as Eq. 1, or models with coupled fast–slow dynamics (Rosenzweig and MacArthur 1963, Box 1) that can be reduced to a system with one state variable through a quasi-steady state approximation. Second, both the maximum response rate and the movement rate of the unstable steady state of Eq. 1 remain unaltered as parameter

a changes, which is generally not the case for comprehensive ecological models. Applying this graphical approach on ecological models could therefore lead to erroneous critical rates of change. Finally, the steady lag approach has its limitations, as it can only be applied to models with an autonomous lag equation (Eq. 8). For models other than Eq. 1, the lag generally depends on the changing parameter, meaning that the lag is explicitly time dependent and a steady lag cannot be assumed.

In the Supplementary material Appendix C and D we apply both analyses on the ecological model by Rosenzweig and MacArthur (1963, Box 1) to study whether the discussed limitations do indeed result in significant errors when applying the analyses to assess critical rates of change in parameters of ecological models. Both analyses yield a critical rate of change in parameter r of $dr/dt = -1.5 \times 10^{-3} \text{ day}^{-2}$ or:

$$\frac{dr}{dt} = \epsilon r \left(\frac{ea(K - R_h)}{K - R_h} - m \right) \quad (11)$$

This value indeed differs from the critical rate of change of $dr/dt = -2 \times 10^{-3} \text{ day}^{-2}$ found through model runs (Fig. 3c). This suggests that, although helpful for identifying the general mechanisms behind rate sensitivity, the presented analyses can only be applied to a limited subset of models.

Identifying real rate sensitive ecosystems

While the critical thresholds that are responsible for change-induced transitions can be found relatively easily using steady state analysis, critical rates of change are more difficult to detect, as pointed out in the previous section. As a result, the identification of rate sensitive models and ultimately of rate sensitive ecosystems will be more challenging. There are, however, some common features of rate sensitive models that may be useful in doing so, as we will discuss in this section.

In contrast to change-induced critical transitions, ecosystems that respond slowly to environmental change are more sensitive to rate-induced critical transitions. This means that ecosystems with at least one slow state variable are more likely to exhibit rate-induced transitions. Such transitions may however not significantly affect the slow variable (Hughes et al. 2013), but may be prominent in a fast state variable with which it interacts. In the model by Rosenzweig and MacArthur (1963, Box 1) for example, the slow consumers fail to cope with their declining resource, leading to overconsumption and a collapse in resource density. Other examples are the model by Luke and Cox (2011) with slow soil carbon dynamics and fast soil temperature dynamics and the model by Scheffer et al. (2008) with slow herbivore and fast plant dynamics, discussed in section ‘Rate-induced critical transitions’. In these models the fast variables have hump-shaped isoclines. This means that the fast variables are controlled by non-linear processes. In the model by Rosenzweig and MacArthur (1963) for instance, both the logistic growth of the resource and its consumption are non-linear processes and in the model by Luke and Cox (2011) the soil carbon decomposition rate increases exponentially with soil temperature. These examples suggest that ecosystems that have coupled slow and fast non-linear processes may be more likely to undergo rate-induced critical transitions.

Models with coupled fast–slow dynamics are also known to exhibit repetitive catastrophic shifts, as previously mentioned. These systems have the same properties as the rate sensitive systems described above, but are in an unstable regime. Ecosystems in which such cyclic dynamics have been observed may therefore be rate sensitive under slightly different environmental conditions. Observing such dynamics at one location may therefore be an indicator that elsewhere along an environmental gradient the ecosystem is rate sensitive. In coastal dune ecosystems for example, water repellency of soils results in nonlinear soil water dynamics (Dekker and Jungerius 1990, Dekker and Ritsema 1994). In these ecosystems the combination of slow plant dynamics and soil water repellency is thought to drive repetitive catastrophic shifts under some conditions and to trigger rate-induced critical transitions in response to declining precipitation under other conditions (Siteur et al. 2016).

Recent studies suggest that ecosystems with spatially periodic patterns may exhibit rate dependent behaviour (Sherratt 2013, Siteur et al. 2014b, Chen et al. 2015). Such patterns are ubiquitously observed in arid ecosystems (Deblauwe et al. 2008), which are currently undergoing rapid climatic changes (Tebaldi et al. 2006, Siteur et al. 2014a). In periodically patterned ecosystems patches of consumers (e.g. plants) compete for a limiting resource (e.g. water). As resource input declines, patches go extinct and the remaining patches rearrange to regain an optimal periodic pattern. If the rearrangement process occurs slowly with respect to the rate of decrease in resource input, a large fraction or even all of the patches may go extinct simultaneously. This is caused by a delayed transition, which forces the model to cross a so-called period-doubling bifurcation (Siteur et al. 2014b, Siero et al. 2015). Rate sensitivity of spatially extended models suggests that spatially periodic patterns could serve as an indicator of real rate sensitive ecosystems.

The common properties of rate sensitive models could be used to determine the ability of ecosystems to undergo rate-induced critical transitions. To assess their susceptibility to rate-induced transitions, one could estimate the recovery rate of ecosystems to perturbations. As shown in Box 2 for the model described by Eq. 1, ecosystems can be expected to become slower in recovering from perturbations when rates of change approach critical rates of change. When subject to natural variability, this could lead to increasing temporal autocorrelation and variance in an ecosystem's state variables. In addition, low diversity and high connectivity are architectural features are known to make ecological networks susceptible to critical transitions (Scheffer et al. 2012). Finally, the susceptibility of ecosystems to rate-induced critical transitions could be assessed using the mechanistic insights provided by the analyses in section 'Analysis of rate sensitive models'. For example, maximum observed response rates in experiments or time series of real ecosystems could be used to assess the susceptibility of ecosystems to rate-induced critical transitions. Note that these types of analyses are now already being applied to real ecosystems (Carpenter et al. 2011, 2014), and could be extended to specifically study rate-induced critical transitions.

Discussion and conclusions

Current anthropogenic environmental changes occur at unprecedented rates (Joos and Spahni 2008, Kaplan et al. 2011, Klein Goldewijk et al. 2011). In this paper we presented and discussed models that suggest that, for some ecosystems, rates of environmental change may be too high to cope with, thereby triggering a new type of critical transition. These rate-induced critical transitions are challenging to analyse in ecological models, but can be understood in elementary models by applying graphical analyses or by studying the lag behind a system's stable steady state. These analyses revealed that 1) rate-induced critical transitions occur if the rate of environmental change is high compared to the response rate of ecosystems, 2) rate-induced critical transitions are similar to change-induced critical transitions but are driven by rates, rather than magnitudes, of environmental change and 3) rate-induced critical transitions occur once a critical rate of change is exceeded. Identification of rate-sensitive ecosystems would also be challenging, but common features of rate-sensitive models suggest that ecosystems with coupled fast-slow dynamics, exhibiting repetitive catastrophic shifts or spatially periodic patterns are more likely to display rate-induced critical transitions.

Although we have suggested a number of common features of rate sensitive models which may be useful in identification of rate sensitive ecosystems, disentangling change- and rate-induced critical transitions in observations would still be challenging. Indeed, to our knowledge no observations of rate-induced critical transitions in real ecosystems have been reported. Rate dependent outcomes have however been reported in a number of experimental studies. Rate dependency is a well known problem for short-term experimental studies on the effect of the relatively gradual rise in atmospheric CO₂ on ecosystem structure and functioning (Luo and Reynolds 1999, Klironomos et al. 2005, Luo and Hui 2009). For example, Klironomos et al. (2005) have found that increasing the CO₂ concentrations instantly from 350 to 550 ppm resulted in a significantly different soil mycorrhizal community structure, whereas the same magnitude of change applied over a period of about six years had no significant effect. There is no reason to believe that such rate dependencies at the community level would have no effects at the ecosystem level, meaning that these experiments do not rule out the possibility of rate sensitivity of real ecosystems.

By using ordinary differential equations to model ecosystems, we implicitly assumed that ecosystems can only respond to environmental changes by adjusting the levels of their state variables. For example, consumers in the model by Rosenzweig and MacArthur (1963, Box 1), only respond to the declining resource density by lowering their own density. In real ecosystems however, populations are known to adapt to environmental changes in other ways too, namely by 1) evading to more suitable habitats or by adapting in situ through 2) phenotypic plasticity and/or through 3) micro-evolutionary adaptation (Holt 1990). The rates of these three alternative response mechanisms are bounded, potentially leading to additional critical rates of environmental change. For example, Devictor et al. (2012) found

Box 2

Generic early-warning signals for rate-induced critical transitions

As systems approach critical thresholds, they become increasingly slow in recovering from perturbations (Wissel 1984, Scheffer et al. 2009). This phenomenon, known as “critical slowing down”, is expected to result in increasing variance and autocorrelation in systems that are subject to natural variability. Figure 6 shows that these early-warning signals also precede the rate-induced critical transition found for the model of Eq. 1. The increases in recovery time, autocorrelation and variance are both predicted by the steady lag analysis (red curves) and model runs (blue crosses), but can not be regarded as trivial since attening of the potential landscape associated with critical slowing down (Scheffer et al. 2009) does not occur as the rate of change approaches its critical value (Fig. 2b).

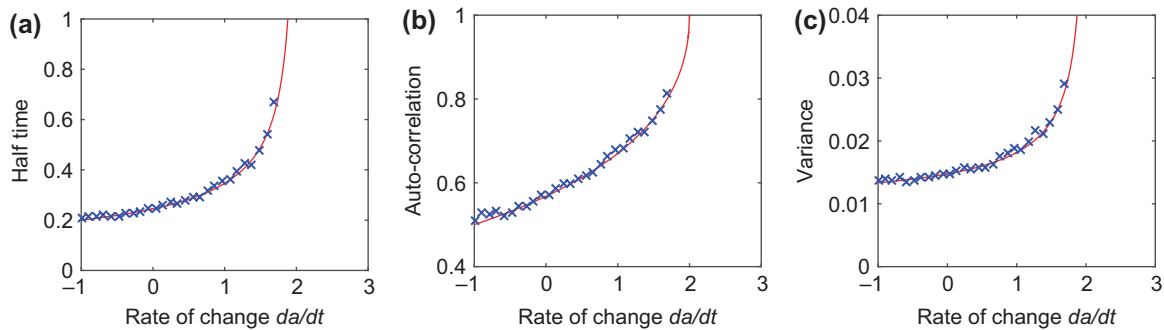


Figure 6. Increasing recovery time from perturbations (a), lag-1 auto-correlation (b) and variance (c) in state variable x of Eq. 1 as the rate of change in parameter a approaches a critical rate of change of $da/dt = 2 (= b)$. The crosses represent the value of each statistic on detrended time series of x with a length of $t = 2000$. State variable x was perturbed with Gaussian noise with a standard deviation of $\sigma = 0.1$, which was applied with an interval of $\Delta t = 0.2$. The curves are derived by linearization around the steady lags.

The half time is given by $t_b = \frac{1}{\lambda} \ln\left(\frac{1}{2}\right)$, with $\lambda = -2\sqrt{b-r}$ (Supplementary material Appendix B), the auto-correlation is given by $\alpha = e^{\lambda\Delta t}$ and the variance by $\text{VAR} = \frac{\sigma^2}{1-\alpha^2}$.

that butterfly and bird populations in Europe do not meet the required displacement velocities to track shifting temperatures, and are building up what they call a “climatic debt”. Also micro-evolutionary adaptation has a limited rate, and theory suggests that critical rates of environmental change exist beyond which selective pressures become too high for positive population growth to be maintained (Lynch and Lande 1993, Bürger and Lynch 1995, Chevin et al. 2010). In order to predict the effect of rapid environmental changes on ecosystems, both the mechanisms behind rate-induced critical transitions on ecosystem level and behind the alternative responses on population level need to be understood.

The focus of steady-state analysis on long-term asymptotic behaviour of ecosystems is sometimes inappropriate and does not always match with ecologically relevant time scales (Hastings 2004, Hughes et al. 2013). Our study shows that steady state analysis is also insufficient to study rate-induced critical transitions. Steady state analysis has shaped the common view on concepts like ecological resilience, as we have pointed out earlier. Definitions of resilience (Holling 1973) are based on the view that ecosystems may shift to alternative dynamics when (external) change or perturbations drive ecosystems beyond a critical threshold. Hence a critical magnitudes of external change and disturbances can be regarded as measures for resilience (Fig. 1a). However, these definitions and measures do not apply to rate sensitive ecosystems, which may

or may not cope with a magnitude of change depending on the time scale over which the change occurs. This suggests that in some cases a broader definition of resilience that acknowledges critical rates of change would be more applicable.

The idea of alternative stable states and critical thresholds in ecosystems has motivated formulation of preconditions for human development on a global scale referred to as “planetary boundaries” (Rockström et al. 2009, Scheffer 2015, Steffen et al. 2015). The proposed boundaries are however all critical levels (e.g. atmospheric carbon dioxide concentration) or rates controlling levels (e.g. the rate of phosphorous mining which controls phosphorous concentrations in the oceans). Rate sensitivity found in models suggests that, given the elevated rates of change in the environment that accompany human development, defining boundaries based on critical levels may not be enough to ensure a safe operating space. In order to define critical rates of change on ecosystem level or even on a global level and to identify rate sensitive systems, a better mechanistic understanding of rate-induced critical transitions is needed.

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Supplementary material (available online as Appendix oik-03112 at <www.oikosjournal.org/appendix/oik-03112>). Appendix A–D.