

## **Ecosystem Resilience and the Paradox of Enrichment**

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### **Abstract**

Regime shifts in complex systems are characterised by abrupt transitions between alternative persistent states. Decreasing resilience (the ability of a system to resist change) has been suggested as a useful leading indicator of regime shifts in such systems. The “paradox of enrichment” is a classic ecological model predicting that ecosystem enrichment can lead to a regime shift to an undesirable state. Here we provide a general mathematical proof that decreasing resilience is a leading indicator of regime shift in the paradox of enrichment. We find that the indicator is more useful in systems where: (1) the prey population growth rate is low; (2) the predation rate is high; and/or (3) predator-prey biomass conversion is efficient. These results can help identify ecosystems in which decreasing resilience is most likely to be a useful leading indicator of regime shift.

### **INTRODUCTION**

Regime shifts in complex systems are characterised by abrupt transitions between alternative persistent states. In ecosystems, such shifts may be associated with ecological and economical damages that are severe, costly and permanent on timescales relevant to human activity (Scheffer & Carpenter 2003). Examples of regime shift are desertification (Rietkerk & van de Koppel 1997; Foley *et al.* 2003), lake eutrophication (Scheffer *et al.* 1997; Carpenter *et al.* 1999), loss of coral reefs to macroalgae (Done 1992; Knowlton 1992; McCook 1999), replacement of woodlands by open grass landscape and vice versa (Dublin *et al.* 1990), and changes in the world’s ocean-climate system (Reid *et al.* 1998; Hare & Mantua 2000; Hsieh *et al.* 2005).

Ecosystems are subject to a variety of external conditions (changes in temperature, water supply, nutrients level, harvesting activities, etc.) most of which vary gradually with time. A regime shift typically follows a period of apparent ecosystem insensitivity to changes in input variables; the shift occurs only when inputs reach a critical threshold (Scheffer & Carpenter 2003). Regime shifts are difficult to predict, because they originate from multiple causes that may act non-linearly at different spatial and temporal scales (Brock & Carpenter 2006). In ecosystems, regime shifts pose a substantial challenge to conservation managers, because warning signals are hard to infer from field observations and empirical data.

Recently, decreasing resilience has been proposed as a signal of impending regime shift in complex systems (Scheffer *et al.* 2001; Scheffer & Carpenter 2003). Resilience is the ability of a system to resist change (Holling 1973). Conceptually, resilience can be viewed as the depth of the basin of attraction surrounding a stable equilibrium. Gradual alterations of the external conditions can make the basin shallower without modifying the equilibrium state. As such, the system has not changed in appearance but has become highly susceptible to further changes that may push it to an alternative stable state (Scheffer & Carpenter 2003).

In the present paper, we investigate the conditions under which resilience is a reliable indicator of regime shift in a classic ecological model, “the paradox of enrichment”. This

model predicts that ecosystem enrichment can cause a regime shift to an undesirable state (Rosenzweig 1971). We provide a general mathematical proof that decreasing resilience is indeed a leading indicator of regime shift in this scenario. We also find that the indicator is more useful in systems where: (1) the prey population growth rate is low; (2) the predation rate is high; and/or (3) predator-prey biomass conversion is efficient. These results can help identify ecosystems in which decreasing resilience is most likely to be a useful leading indicator of regime shift.

## METHODS AND RESULTS

A classic dynamical system in ecology is the two-species predator-prey model used by Rosenzweig (1971) to demonstrate the paradox of enrichment. The results of Rosenzweig's model caution against enrichment as a strategy for increasing yields from ecosystems. Rosenzweig provides six alternative formulations of the model, one of which is given by the following equations:

$$\frac{dV}{dt} = rV \left( 1 - \frac{V}{K} \right) - kP(1 - e^{-cV}) \quad (1)$$

$$\frac{dP}{dt} = AkP(e^{-cJ} - e^{-cV}) \quad (2)$$

where  $V$  is the population size of the prey species,  $P$  is the population size of the predator species,  $r$  is the population growth rate of the prey species,  $K$  is the carrying capacity of the prey species,  $k$  is the predation rate,  $c$  is a constant to account for density-dependent predation effects (for small values of  $c$ , predation rates are lower at low prey density),  $J$  is the population size of the prey at equilibrium and  $A$  is the predator-prey conversion efficiency.

Rosenzweig (1971) showed that the nontrivial equilibrium of this system is stable for values of  $K$  below a certain threshold, but becomes unstable past this point. Thus, attempting to increase the carrying capacity of the system by, for example, increasing the supply of a limiting nutrient, can actually lead to a Hopf bifurcation, destabilising the system and resulting in extinction of both predator and prey.

The nontrivial equilibrium of the system given by equations (1) and (2) is given by the following expressions (Rosenzweig 1971):

$$\bar{V} = J$$

$$\bar{P} = \frac{rJ(1 - J/K)}{k(1 - e^{-cJ})}$$

The equilibrium exists ( $\bar{P}$  is positive) when  $K > J$ .

To investigate stability we construct the Jacobian matrix of partial derivatives and evaluate it at the equilibrium:

$$\Gamma = \begin{bmatrix} \frac{\partial(dP/dt)}{\partial P} & \frac{\partial(dV/dt)}{\partial P} \\ \frac{\partial(dP/dt)}{\partial V} & \frac{\partial(dV/dt)}{\partial V} \end{bmatrix}_{V=\bar{V}, P=\bar{P}}$$

$$\Gamma = \begin{bmatrix} 0 & -k(1 - e^{-cJ}) \\ cak\bar{P}e^{-cJ} & r - 2r\frac{J}{K} - ck\bar{P}e^{-cJ} \end{bmatrix}$$

The system is stable when the determinant of the Jacobian is positive and the trace is negative (Jury criteria). The determinant of  $\Gamma$  is easily shown to be always positive when the equilibrium exists. The trace is negative when the term at the lower right of the matrix is negative. This can be shown to be true when the following condition is satisfied (Rosenzweig 1971):

$$K < K_{crit} = \frac{J(2e^{cJ} - cJ - 2)}{e^{cJ} - cJ - 1}$$

The resilience of the system (the ability of the system to resist change),  $\rho$ , can be expressed in terms of the time to return to equilibrium after a small perturbation (Nakajima & DeAngelis 1989):

$$T_R = \frac{1}{|\text{Re}(\lambda_{dom})|}$$

$$\rho = \frac{1}{T_R} = |\text{Re}(\lambda_{dom})|$$

where  $\lambda_{dom}$  is the dominant eigenvalue of the Jacobian (the eigenvalue with greatest real part). Thus, to calculate resilience, we need to calculate the eigenvalues of the Jacobian. Let:

$$\beta = -k(1 - e^{-cJ})$$

$$\gamma = cAk\bar{P}e^{-cJ}$$

$$\delta = r - 2r\frac{J}{K} - ck\bar{P}e^{-cJ}$$

Then the eigenvalues of the Jacobian are given by:

$$\lambda = \frac{\delta \pm \sqrt{\delta^2 + 4\beta\gamma}}{2}$$

The real part of the dominant eigenvalue is then given by:

$$\text{Re}(\lambda_{dom}) = \begin{cases} \delta/2, & \delta^2 + 4\beta\gamma < 0 \\ \frac{\delta + \sqrt{\delta^2 + 4\beta\gamma}}{2}, & \delta^2 + 4\beta\gamma > 0 \end{cases}$$

We are interested in how the resilience,  $|\text{Re}(\lambda_{dom})|$ , changes as  $K$  increases. In the stable regime, the real part of the  $\lambda$  dominant eigenvalue is negative, so we can take resilience as  $\rho = -\text{Re}(\lambda_{dom})$ .

If  $\delta^2 + 4\beta\gamma < 0$ , then:

$$\frac{d\rho}{dK} = -\frac{1}{2} \frac{d\delta}{dK} \tag{3}$$

and

$$\begin{aligned}\frac{d\delta}{dK} &= 2r \frac{J}{K^2} - \frac{d\bar{P}}{dK} cke^{-cJ} \\ \frac{d\bar{P}}{dK} &= \frac{rJ}{k(1-e^{-cJ})} \frac{J}{K^2} \\ \Rightarrow \frac{d\delta}{dK} &= r \frac{J}{K^2} \left\{ 2 - \frac{cJ}{e^{cJ} - 1} \right\} > 0\end{aligned}$$

The inequality follows from a Taylor expansion of  $e^{cJ}$  and the fact that  $c$  and  $J$  are positive. This leads directly to:

$$\frac{d\rho}{dK} < 0, \text{ for } \delta^2 + 4\beta\gamma < 0$$

If  $\delta^2 + 4\beta\gamma > 0$ , then:

$$\begin{aligned}\frac{d\rho}{dK} &= -\frac{1}{2} \frac{d\delta}{dK} - \frac{1}{4} \left\{ 2\delta \frac{d\delta}{dK} + 4\beta \frac{d\gamma}{dK} \right\} \frac{1}{\sqrt{\delta^2 + 4\beta\gamma}} \\ &= -\frac{1}{2} \left( \left\{ 1 + \frac{\delta}{\sqrt{\delta^2 + 4\beta\gamma}} \right\} \frac{d\delta}{dK} + \frac{2\beta}{\sqrt{\delta^2 + 4\beta\gamma}} \frac{d\gamma}{dK} \right)\end{aligned}\quad (4)$$

Also:

$$\frac{d\gamma}{dK} = cAke^{-cJ} \frac{d\bar{P}}{dK} = \frac{cArJ^2}{(e^{cJ} - 1)K^2} > 0$$

Thus the two derivatives  $d\delta/dK$  and  $d\gamma/dK$  in equation (4) are positive, and the two coefficients of the derivatives are readily shown to be negative, so the whole expression is positive:

$$\frac{d\rho}{dK} > 0, \text{ for } \delta^2 + 4\beta\gamma > 0$$

Thus, for  $\delta^2 + 4\beta\gamma < 0$ , resilience is decreasing, whereas for  $\delta^2 + 4\beta\gamma > 0$ , resilience is increasing.

There is some value of  $K = K_r$  for which  $\delta^2 + 4\beta\gamma = 0$ . It is easily shown that  $d(\delta^2 + 4\beta\gamma)/dK < 0$ , so for  $K < K_r$  resilience is increasing and for  $K > K_r$  resilience is decreasing. The graph of resilience versus  $K$  is unimodal with the maximum at  $K = K_r$  (Figure 1). The system bifurcates at  $K = K_{crit}$  and it can be shown that  $K_r$  is always strictly less than  $K_{crit}$ :

$$\begin{aligned}K_r &= \frac{J\alpha}{(\alpha - 1) + \frac{2}{\alpha} \left( -\tau + \sqrt{\tau(\alpha + \tau)} \right)} \\ &= \frac{J\alpha}{(\alpha - 1) + \frac{2}{\alpha} \left( \sqrt{\tau^2 - \tau\alpha} - \tau \right)} < \frac{J\alpha}{(\alpha - 1)} = K_{crit}\end{aligned}$$

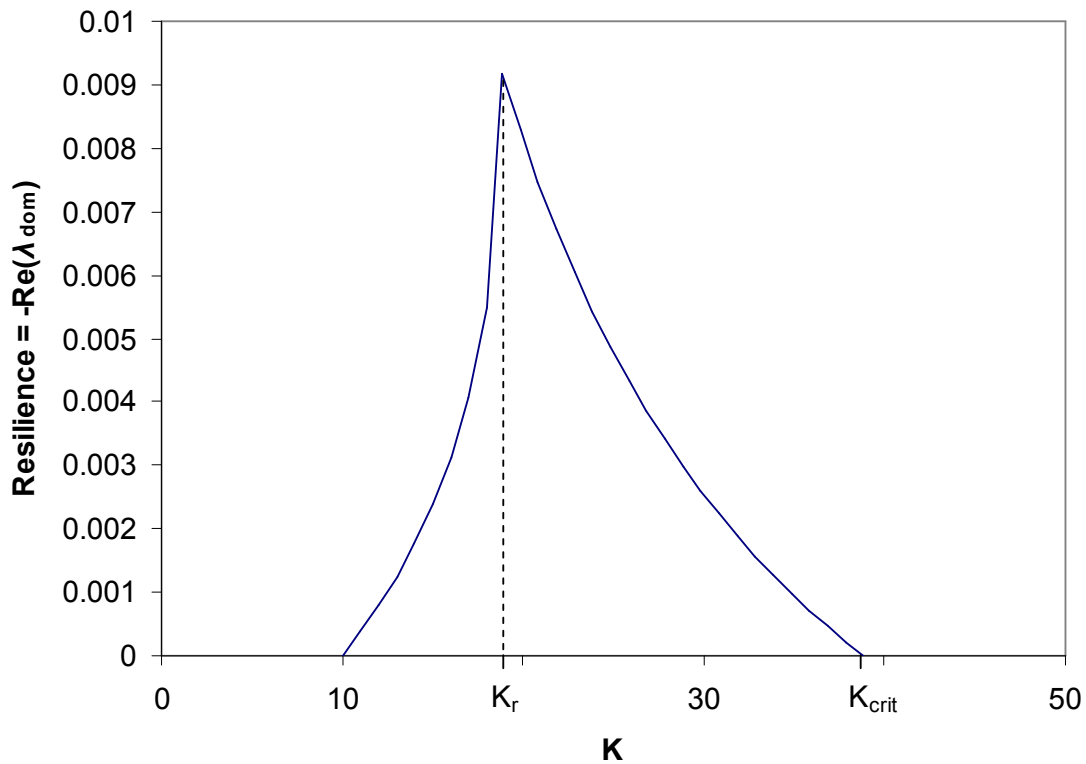
where:

$$\tau = \frac{Ake^{-cJ}cJ}{r} > 0$$

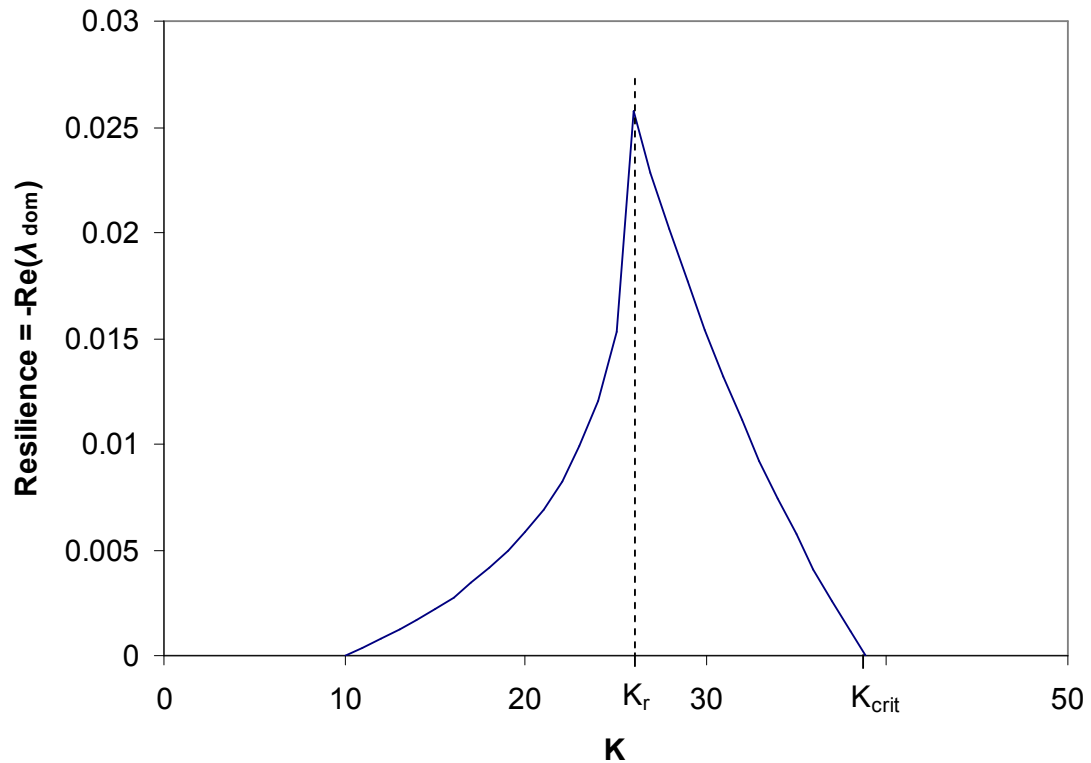
$$\alpha = 2 - \frac{cJ}{e^{cJ} - 1} > 0$$

Thus, resilience will always decrease before the critical threshold is reached and we will have some warning of the impending bifurcation. However, if  $K_r$  is close to  $K_{crit}$  then the warning period will be short. This is the case when  $\tau \rightarrow 0$ , or when  $r \rightarrow \infty$ ,  $k \rightarrow 0$ ,  $cJ \rightarrow 0$  or  $A \rightarrow 0$ . This means that in systems where the growth rate of the prey population is high ( $r \rightarrow \infty$ ), the predation rate is low ( $k \rightarrow 0$ ;  $cJ \rightarrow 0$ ), or predator-prey biomass conversion is inefficient ( $A \rightarrow 0$ ), we can expect little warning of the impending bifurcation. Conversely, when the growth rate of the prey is low (Figure 2), the predation rate is high, or the predator-prey biomass conversion is efficient, we may have considerable warning of impending bifurcation, and resilience may be a useful leading indicator of regime shift.

For Rosenzweig's five other predator-prey models, we obtain similar qualitative results. These are given in the Appendix.



**Figure 1** Resilience versus carrying capacity ( $K$ ) for the two-species predator-prey model specified by equations (1) and (2) with  $k = 0.05$ ,  $c = 0.08$ ,  $r = 0.05$ ,  $J = 10$  and  $A = 0.2$ . The decreasing resilience in the region  $K_r < K < K_{crit}$  provides a warning of the impending bifurcation and destabilisation of the system at  $K = K_{crit}$ .



**Figure 2** As for Figure 1, but with the prey population growth rate,  $r = 0.3$ . The effect of increasing  $r$  is to move  $K_r$  closer to  $K_{\text{crit}}$  and thereby contract the range of values of  $K$  over which decreasing resilience is observed. This means that there is less warning of the impending bifurcation at  $K_{\text{crit}}$ .

## DISCUSSION

Here we have produced two main results concerning resilience and the paradox of enrichment. Firstly, our general analytical results show that resilience is a leading indicator of regime shift in each of the six different two-species models used by Rosenzweig (1971). This extends the result of Nakajima and DeAngelis (1989), who obtained a similar result based on a single parameterisation of a similar two-species model. Secondly, we have identified circumstances under which resilience is more likely to be a useful indicator of regime shift in simple two-species models.

We identify three avenues for future research: analytic treatment of more complicated models; empirical valuation of our predictions using computer models; and empirical validation of our predictions using real ecosystems.

Further analytic work is required to investigate whether our results apply to more complicated models that are closer analogues of real-world ecosystems. Nakajima and DeAngelis (1989), for instance, extend the paradox of enrichment to a three-parameter model that includes nutrient recycling and find that, for their parameterisation at least, resilience decreases only shortly before the regime shift, because the third eigenvalue introduced by the third differential equation dominates the dynamics of the system for most nutrient input levels. In such cases, our conditions for resilience to be a useful leading indicator of regime shift may not apply.

Empirical validation of our results is necessary because in practice the signal of decreasing resilience may be masked by noise and difficult to measure. One measure of resilience in modelling studies is variance (Brock & Carpenter 2006). Increasing variance is associated with decreasing resilience because, as a system becomes less resilient, it takes longer to recover from small perturbations and the overall behaviour is more variable. An investigation into whether the increasing variance signal is stronger in empirical models with low prey growth rates, high predation rates and/or efficient predator-prey biomass conversion would provide an empirical test of our theoretical results. Our preliminary investigations in this direction have thus far been equivocal.

Our predictions about the kinds of ecosystems in which resilience is a useful leading indicator of regime shift are, in principle, empirically testable with data from real ecosystems. Examples of such ecosystems are lakes enriched by nutrient run-off (Carpenter 2003; Carpenter & Brock 2006), and the two-species aquatic laboratory communities that have previously been used to investigate the paradox of enrichment (Fussmann *et al.* 2000; Fussmann *et al.* 2005).

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**Appendix to Ecosystem Resilience and the Paradox of Enrichment****Table A.1** Analysis of Rosenzweig's (1971) models 1-6, following the procedure described for model 4 in the main text.

Model <sup>1</sup>	1	2	3
<b>Prey equation</b>	$\frac{dV}{dt} = rV(RV^{-a} - Q) - kP(1 - e^{-cV})$	$\frac{dV}{dt} = rV\left(1 - \frac{V}{K}\right) - kPV^g$	$\frac{dV}{dt} = rV(RV^{-a} - Q) - kPV^g$
<b>Predator equation</b>	$\frac{dP}{dt} = AkP(e^{-cJ} - e^{-cV})$	$\frac{dP}{dt} = AkP(V^g - J^g)$	$\frac{dP}{dt} = AkP(V^g - J^g)$
<b>Non-trivial equilibrium</b>	$\bar{V} = J$ $\bar{P} = \frac{rJ(RJ^{-a} - Q)}{k(1 - e^{-cJ})}$	$\bar{V} = J$ $\bar{P} = \frac{rJ^{1-g}(1 - J/K)}{k}$	$\bar{V} = J$ $\bar{P} = \frac{r}{k}J^{1-g}(RJ^{-a} - Q)$
<b>Jacobian</b>	$\Gamma = \begin{bmatrix} 0 & -k(1 - e^{-cJ}) \\ cak\bar{P}e^{-cJ} & r\{(1-a)RJ^{-a} - Q\} - ck\bar{P}e^{-cJ} \end{bmatrix}$	$\Gamma = \begin{bmatrix} 0 & -kJ^g \\ Ak\bar{P}gJ^{g-1} & r - 2r\frac{J}{K} - kg\bar{P}J^{g-1} \end{bmatrix}$	$\Gamma = \begin{bmatrix} 0 & -kJ^g \\ Akg\bar{P}J^{g-1} & r(1-a)RJ^{-a} - rQ - kg\bar{P}J^{g-1} \end{bmatrix}$
<b>Definitions</b>	$\alpha = 1 - \frac{cJ}{e^{cJ} - 1} > 0$ $\tau = \frac{2Ake^{-cJ}cJ}{r(\alpha - a)} > 0$	$\tau = \frac{4AkgJ^g}{r} > 0$	$\alpha = \frac{1 - g - a}{a} > 0$ $\tau = \frac{4kgAJ^g}{ra^2\alpha^2} > 0$
<b><math>K_{crit}</math> or <math>R_{crit}</math></b>	$R_{crit} = \frac{QJ^a(e^{cJ} - 1 - cJ)}{(e^{cJ} - 1)(1 - a) - cJ} = \frac{J^a\alpha Q}{\alpha - a}$ Note: $R_{crit}$ only exists for $\alpha - a > 0$	$K_{crit} = \frac{J(g - 2)}{g - 1}$	$R_{crit} = QJ^a\left(\frac{1 - g}{1 - g - a}\right) = QJ^a\left(1 + \frac{a}{\alpha}\right)$
<b><math>K_r</math> or <math>R_r</math></b>	$R_r = \frac{J^a}{\alpha - a} \left\{ \alpha Q + \tau - \sqrt{\tau^2 + 2Qa\tau} \right\}$ $< \frac{J^a\alpha Q}{\alpha - a} = R_{crit}$	$K_r = \frac{J(g - 2)}{g - 1 + \frac{1}{2(g - 2)} \left\{ \sqrt{\tau^2 + 4\tau(2 - g)} - \tau \right\}}$ $< \frac{J(g - 2)}{g - 1} = K_{crit}$	$R_r = J^a \left( Q \left( 1 + \frac{1}{\alpha} \right) + \frac{\tau}{2} - \sqrt{\tau \left( \frac{Q}{\alpha} + \frac{\tau}{4} \right)} \right)$ $< QJ^a \left( 1 + \frac{1}{\alpha} \right) = R_{crit}$

<sup>1</sup> The parameters  $a$  et  $g$  obey:  $0 < g \leq 1$ ,  $0 < a \leq 1$  and  $a + g < 1$ .

Table A.1 continued

Model	4	5	6
<b>Prey equation</b>	$\frac{dV}{dt} = rV \left(1 - \frac{V}{K}\right) - kP(1 - e^{-cV})$	$\frac{dV}{dt} = rV(\ln K - \ln V) - kPV^g$	$\frac{dV}{dt} = rV(\ln K - \ln V) - kP(1 - e^{-cV})$
<b>Predator equation</b>	$\frac{dP}{dt} = AkP(e^{-cJ} - e^{-cV})$	$\frac{dP}{dt} = AkP(V^g - J^g)$	$\frac{dP}{dt} = AkP(e^{-cJ} - e^{-cV})$
<b>Non-trivial equilibrium</b>	$\bar{V} = J$ $\bar{P} = \frac{rJ(1 - J/K)}{k(1 - e^{-cJ})}$	$\bar{V} = J$ $\bar{P} = \frac{r}{k} J^{1-g} (\ln K - \ln J)$	$\bar{V} = J$ $\bar{P} = \frac{r}{k} J \frac{(\ln K - \ln J)}{(1 - e^{-cJ})}$
<b>Jacobian</b>	$\Gamma = \begin{bmatrix} 0 & -k(1 - e^{-cJ}) \\ cAk\bar{P}e^{-cJ} & r - 2r\frac{J}{K} - ck\bar{P}e^{-cJ} \end{bmatrix}$	$\Gamma = \begin{bmatrix} 0 & -kJ^g \\ Akg\bar{P}J^{g-1} & r(\ln K - \ln J - 1) - kg\bar{P}J^{g-1} \end{bmatrix}$	$\Gamma = \begin{bmatrix} 0 & -k(1 - e^{-cJ}) \\ ckA\bar{P}Je^{-cJ} & r(\ln K - \ln J - 1) - ck\bar{P}e^{-cJ} \end{bmatrix}$
<b>Definitions</b>	$\tau = \frac{Ake^{-cJ}cJ}{r} > 0$ $\alpha = 2 - \frac{cJ}{e^{cJ} - 1} > 0$	$\alpha = 1 - g > 0$ $\tau = \frac{4AkgJ^g}{r\alpha^2} > 0$	$\alpha = 1 - \frac{cJ}{e^{cJ} - 1} > 0$ $\tau = \frac{4AkcJ^2e^{-cJ}}{r\alpha^2} > 0$
<b><math>K_{crit}</math> or <math>R_{crit}</math></b>	$K_{crit} = \frac{J(2e^{cJ} - cJ - 2)}{e^{cJ} - cJ - 1}$	$\ln K_{crit} = \ln J + \frac{1}{1-g} = \ln J + \frac{1}{\alpha}$	$\ln K_{crit} = \ln J + 1 + \frac{cJ}{e^{cJ} - 1 - cJ} = \ln J + \frac{1}{\alpha}$
<b><math>K_r</math> or <math>R_r</math></b>	$K_r = \frac{J\alpha}{(\alpha - 1) + \frac{2}{\alpha} \left( \sqrt{\tau^2 - \tau\alpha - \tau} \right)}$ $< \frac{J\alpha}{(\alpha - 1)} = K_{crit}$	$\ln K_r = \ln J + \frac{1}{\alpha} + \frac{\tau}{2} - \sqrt{\tau \left( \frac{1}{\alpha} + \frac{\tau}{4} \right)}$ $< \ln J + \frac{1}{\alpha} = \ln K_{crit}$	$\ln K_r = \ln J + \frac{1}{\alpha} + \frac{\tau}{2} - \sqrt{\tau \left( \frac{1}{\alpha} + \frac{\tau}{4} \right)}$ $< \ln J + \frac{1}{\alpha} = \ln K_{crit}$