Critical slowing down as an indicator of transitions in two-species models

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A B S T R A C T

Transitions in ecological systems often occur without apparent warning, and may represent shifts between alternative persistent states. Decreasing ecological resilience (the size of the basin of attraction around a stable state) can signal an impending transition, but this effect is difficult to measure in practice. Recent research has suggested that a decreasing rate of recovery from small perturbations (critical slowing down) is a good indicator of ecological resilience. Here we use analytical techniques to draw general conclusions about the conditions under which critical slowing down provides an early indicator of transitions in two-species predator–prey and competition models. The models exhibit three types of transition: the predator–prey model has a Hopf bifurcation and a transcritical bifurcation, and the competition model has two saddle-node bifurcations (in which case the system exhibits hysteresis) or two transcritical bifurcations, depending on the parameterisation. We find that critical slowing down is an earlier indicator of the Hopf bifurcation in predator–prey models in which prey are regulated by predation rather than by intrinsic density-dependent effects and an earlier indicator of transitions in competition models in which the dynamics of the rare species operate on slower timescales than the dynamics of the common species. These results lead directly to predictions for more complex multispecies systems, which can be tested using simulation models or real ecosystems.

1. Introduction

Transitions in ecological systems may be associated with ecological and economic damages that are severe, costly and permanent on timescales relevant to human activity (Scheffer and Carpenter, 2003). Of particular concern are systems that exhibit hysteresis, meaning that alternative stable states exist and that the current state depends on the history of the system (van Nes and Scheffer, 2005). Examples of systems that exhibit hysteresis include desertification (Foley et al., 2003; Rietkerk and van de Koppel, 1997), lake eutrophication (Carpenter et al., 1999; Scheffer et al., 2001), replacement of woodlands by grasslands and vice versa (Dublin et al., 2008; Done, 1992; Knowlton, 1992; McCook, 1999), replacement of coral reefs by macroalgalus (deYoung et al., 2008; Hsieh et al., 2005; Reid et al., 1998). Transitions in systems without hysteresis, such as those that occur between stable equilibria and stable limit cycles in predator–prey models, may also be of concern, because of the potential for oscillatory behaviour to trigger extinction when stochastic forces are at play (May, 1972; Rosenzweig, 1971). Ecosystems are subject to a variety of external conditions (changes in temperature, water supply, nutrient levels, harvesting activities, etc.), most of which vary gradually with time. A transition often follows a period of apparent ecosystem insensitivity to changes in these conditions; the shift occurs only when conditions reach a critical threshold (Scheffer and Carpenter, 2003). Transitions are often difficult to predict, because they can originate from multiple causes that may act non-linearly at different spatial and temporal scales (Brock and Carpenter, 2006). In ecosystems, transitions pose a substantial challenge to conservation managers, because warning signals are hard to infer from field observations and empirical data.

Decreasing ecological resilience has been proposed as a signal of impending transitions in complex systems (Scheffer and Carpenter, 2003; Scheffer et al., 2001). Ecological resilience is the ability of a system to absorb perturbations and persist at a particular stable equilibrium (Holling, 1973; van Nes and Scheffer, 2007). Conceptually, it is the size 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 and Carpenter, 2003).

Ecological resilience cannot be measured directly in practice, and so there is a need for indirect indicators. One potential such indicator is critical slowing down, the decrease in recovery rate that occurs as the basin of attraction around a stable equilibrium shrinks and a system approaches a transition (van Nes and
Scheffer, 2007). For a variety of ecological models, critical slowing down occurs far enough from a threshold to be a potentially useful indicator of an impending transition (van Nes and Scheffer, 2007). A recent analysis of ancient climate changes suggests that slowing down may even be a useful indicator of impending climate change (Dakos et al., 2008).

Here we investigate the circumstances under which critical slowing down is an early indicator of transitions in classic two-species ecological models: a generalised predator–prey model and two versions of the Lotka–Volterra competition model. We chose these models because they are the simplest and most studied two-species models in ecology and are, therefore, a stepping stone to understanding more complex multi-species models. An advantage of our approach over the recent work by van Nes and Scheffer (2007) is that we investigate the models’ behaviour analytically rather than numerically. This enables us to draw general conclusions about the effects of different model parameters on recovery rates and the range of parameter space in which critical slowing down occurs.

2. Methods

We analysed how the recovery rate changes as a transition is approached in three two-species ecological models: a generalised predator–prey model, a Lotka–Volterra competition model parameterised such that coexistence is unstable, and a Lotka–Volterra competition model parameterised such that coexistence is stable. Each model exhibits different types of transition.

The generalised predator–prey model is specified by the following equations:

\[
\begin{align*}
\frac{dP}{dt} &= rPf(V) - kPfh(V) \\
\frac{dV}{dt} &= AkJVf(V) - h(J) 
\end{align*}
\]

where \( t \) is time, \( P \) is prey population size, \( r \) is the intrinsic rate of increase in prey, \( P \) is predator population size, \( k \) is the predation rate, \( f \) is the equilibrium prey population size, and \( A \) is the predator–prey conversion efficiency. The function \( f(V) \) represents the effects of intra-specific competition among the prey: as the prey population increases, the per-capita population growth rate decreases and eventually becomes zero at the carrying capacity, \( K \) (\( f(V) = 0 \) and \( f'(V) < 0 \) for \( 0 < V < K \), and \( f(K) = 0 \)). The carrying capacity, \( K \), is the control parameter. We further assume that \( f \) is an increasing function of \( K \) and that the derivative of \( f \) with respect to \( V \) is a non-decreasing function of \( K \) \( (df/dK) > 0 \), \( df'(V)/dK > 0 \). The function \( h(V) \) represents the per-capita rate at which predators kill prey; the kill-rate increases as the number of available prey increases, but does so at a decreasing rate \( (h(V) > 0 \), \( h'(V) > 0 \) and \( h''(V) < 0 \)). This generalised predator–prey model covers the models given in Rosenzweig (1971) and May (1972), but not the Lotka–Volterra predator–prey model, which does not have a stable equilibrium (May, 1972). The predator–prey model exhibits a transition between a stable equilibrium and a stable limit cycle (a Hopf bifurcation) (May, 1972; Rosenzweig, 1971) and a transcritical bifurcation.

The competition model is specified by the following equations (Lotka, 1925, 1956):

\[
\begin{align*}
\frac{dN_1}{dt} &= \frac{r_1N_1(K_1 - N_1 - z_{12}N_2)}{K_1} \\
\frac{dN_2}{dt} &= \frac{r_2N_2(K_2 - N_2 - z_{21}N_1)}{K_2} 
\end{align*}
\]

where \( t \) is time, \( N_i \) is the abundance of species \( i \), \( r_i \) is the intrinsic rate of increase in species \( i \), \( K_i \) is the carrying capacity of species \( i \), and \( z_{ij} \) is the competitive impact of species \( j \) on species \( i \). The carrying capacity of species 1, \( K_1 \), is the control parameter. Coexistence is unstable when \( z_{12} > \frac{1}{2} \), in which case the model exhibits saddle-node bifurcations from dominance by one species to dominance by the other species and hysteresis occurs. Coexistence is stable when \( z_{12} < \frac{1}{2} \), in which case the model exhibits transcritical bifurcations from coexistence to and from dominance by either species and hysteresis does not occur.

The first step in the analysis of each model was to find the equilibria and the conditions for existence and stability of the equilibria. To find the conditions for stability we linearised each model around its equilibria by constructing the Jacobian matrix of partial derivatives and applying the Routh–Hurwitz criteria for a two-dimensional continuous-time system: an equilibrium is stable when the determinant of the Jacobian evaluated at the equilibrium is positive and the trace of the Jacobian is negative.

For each model, we then calculated the recovery rate as the absolute value of the real part of the dominant eigenvalue, \( \lambda_{\text{dom}} \), of the Jacobian matrix of partial derivatives at each equilibrium (the dominant eigenvalue is the eigenvalue with greatest real part for a continuous system; Nakajima and DeAngelis, 1989; van Nes and Scheffer, 2007):

\[
\rho = |\text{Re}(\lambda_{\text{dom}})|
\]

We investigated how the recovery rate, \( \rho \), varies with respect to a control parameter as the system approaches a transition. For the predator–prey model we used the carrying capacity, \( K \), of the prey as the control parameter. An increase in this parameter could represent enrichment of a lake or other ecosystem by human activities (Rosenzweig, 1971). For the competition model we used the carrying capacity, \( K_i \), of one species as the control parameter (following van Nes and Scheffer, 2007). An increase in this parameter could represent enrichment of a resource that is limiting for one species.

For each model, we identified regions of parameter space in which decreasing recovery rate, or critical slowing down, is a better indicator of a transition with respect to the control parameter. In particular, we were interested in measuring the distance, in terms of each model’s parameters, between the point at which the recovery rate starts to decrease, \( K_i \), and the critical transition, \( K_{\text{crit}} \). This distance can be seen as a warning period of the impending transition. The utility of critical slowing down as a leading indicator of the transition depends crucially on the length of this warning period. Our method can yield general conclusions about the effects of the various parameters on the usefulness of critical slowing down as an indicator of an upcoming transition in a system’s dynamics. To illustrate our analytical results, we also constructed a numerical version of each model in MATLAB.

3. Results

3.1. Two-species predator–prey

This model has three equilibria:

\[
V = 0, \quad P = 0
\]

(4)

\[
V = K, \quad P = 0
\]

(5)

\[
V = J \\
P = \frac{rJf(J)}{kh(J)}
\]

(6)

The trivial equilibrium (4) exists and is unstable for all values of \( K \). The equilibrium with only prey present (5) exists for all values of \( K \), and is stable for \( K < J \). The equilibrium with both prey and
predators present (6) exists (in the sense that $P$ is non-negative) for $K > J$ and is stable for $J < K < K_{crit}$, where $K = K_{crit}$ is the solution of the following (remembering that $f$ is a function of $K$):

$$
\left\{ \begin{array}{l}
1 - \frac{Jf(J)}{h(J)} \int f(J) + Jf'(J) = 0 \\
\end{array} \right.
$$
(7)

At the point $K = J$ a transcritical bifurcation occurs: equilibria (5) and (6) collide and exchange stability properties. At the point $K = K_{crit}$ a Hopf bifurcation occurs: equilibrium (6) becomes unstable and a stable limit cycle emerges (see Appendix A for details).

It can be shown that the maximum recovery rate (see Appendix A) occurs for some value of $K = K_0$, where

$$
\left\{ \begin{array}{l}
1 - \frac{Jf(J)}{h(J)} \int f(J) + Jf'(J) = 2 \sqrt{\frac{Ak_J}{r} h(J)f(J)} \\
\end{array} \right.
$$
(8)

Thus, critical slowing down occurs as $K$ is increased on the approach to the Hopf bifurcation for $K_0 < K < K_{crit}$. If we are using the recovery rate as an indicator of system dynamics, we will have more warning of the impending regime shift when $K$ is far from $K_{crit}$; conversely, we will have less warning when $K$ is close to $K_{crit}$. From Eqs. (7) and (8), we see that $K$ approaches $K_{crit}$ when the right-hand side of (8) approaches zero:

$$
\frac{Ak_J}{r} h(J)f(J) \to 0
$$
(9)

This occurs as $A \to 0$ (predator–prey biomass conversion is inefficient; Fig. 1), $r \to \infty$ (the intrinsic rate of increase in the prey population is high), or $k \to 0$ (the predation rate is low). $K$ also becomes close to $K_{crit}$ when $h(J) \to 0$, meaning that the predation rate increases slowly with increasing prey population size, which is equivalent to the predation rate being low. The parameter $J$ simply scales the whole system, so it does not make sense to consider what happens when $J \to 0$. The converse arguments apply as $K$ decreases on the approach to the transcritical bifurcation at $K = J$ (Fig. 1). There will be less warning of this transition as $A \to \infty$, $r \to 0$, $K \to \infty$ and/or $h(J) \to \infty$.

The behaviour of the system with respect to $f(J)$ is more complicated and depends on the exact form of the functional relationship $f(J)$, because $f(J)$ and its derivative appear on the left hand side of (7) and (8). However, it is clear from the definition of the model, that increasing $f(J)$ by a multiplicative constant will have the same effect as increasing the prey growth rate, $r$.

### 3.2. Two-species competition (coexistence unstable)

The Lotka–Volterra model has four equilibria:

1. $N_1 = K_1$, $N_2 = 0$  \quad (10)
2. $N_1 = 0$, $N_2 = K_2$  \quad (11)
3. $N_1 = 0$, $N_2 = 0$  \quad (12)
4. $N_1 = \frac{K_1 - 21K_2}{1 - 21221}$, $N_2 = \frac{K_2 - 21K_1}{1 - 21221}$  \quad (13)

The trivial equilibrium (12) is always unstable. The equilibrium given by (10) is stable for values of the control parameter $K_1 > K_{221}$; the equilibrium given by (11) is stable for values of the control parameter $K_1 < K_{221}$. When $21221 > 1$, we see that both are present and stable. The single-species dominant equilibria (10) and (11) both exist and are stable for $K_{221} < K_1 < K_{221}$. Saddle-node bifurcations occur at the boundaries of this interval, where the system shifts from dominance by one species to dominance by the other species.

We investigate the transition from dominance by species 1 to dominance by species 2. It can be shown (see Appendix A) that for sufficiently large values of the control parameter, $K_1$, the recovery rate is constant ($\rho = r_1$). As the control parameter decreases, the recovery rate begins to decline at

$$
K_1 = K_r = \left(1 + \frac{r_1}{r_2}\right) \frac{K_2}{K_2^2}
$$
(14)

giving us warning of the impending critical transition at $K_1 = K_{crit} = K_{221}$. When $r_1$ is large relative to $r_2$, $K_r$ is large relative to $K_{221}$ and we get more warning of the critical transition from dominance by species 1 to dominance by species 2 (compare Figs. 2c and d). A similar analysis shows that when $r_2$ is large relative to $r_1$, $K_r$ is small relative to $K_{crit}$ and we get more warning of the reverse critical transition from dominance by species 2 to dominance by species 1 (again, compare Figs. 2c and d).

### 3.3. Two-species competition (coexistence stable)

In this subsection, the Lotka–Volterra model is parameterised such that $21221 < 1$, so the coexistence equilibrium (13) exists when $21221 < K_1 < K_{221}$. It can be shown (see Appendix A) that the recovery rate has its maximum with respect to the control parameter, $K_1$, at approximately

$$
K_1 = K_r = K_2 \times \sqrt{\frac{21221}{2121 + 221}}
$$
(15)

To establish when decreasing recovery rate is an early indicator of an impending transition, we are interested in the position of $K_r$, the value of the control parameter for which recovery rate is a maximum, relative to the values of the control parameter at which the transitions occur: $K_1 = K_{crit,1} = 21221$ and $K_1 = K_{crit,2} = K_{221}$. From (15), we can see that as $r_1/r_2 \to 0$, $K_r \to K_{221}$, which means that we have less warning of transitions between coexistence and dominance by species 1, but more warning of transitions between coexistence and dominance by species 2 (Fig. 3c). The converse is true for when $r_1/r_2 \to \infty$ (Fig. 3d).

### 4. Discussion

In the analysis of dynamical systems, bifurcations are defined as changes to the qualitative structure of solutions as parameters are varied continuously (Guckenheimer and Holmes, 1997). Local bifurcations include simple bifurcations of individual equilibria and can be analysed using only local information about a system; global bifurcations are changes to a system's properties that cannot be deduced from local information. Critical slowing down, which has been proposed as a leading indicator of transitions in real-world complex systems (van Nes and Scheffer, 2007), can be shown mathematically to occur as any system approaches a local bifurcation (Wissel, 1984). In this paper we have investigated the phenomenon of critical slowing down near local bifurcations of simple two-species models. We did not analyse global bifurcations, which also occur in ecological models (e.g., Ives et al., 2008) but are analytically less tractable and are not generally associated with critical slowing down.

In real-world complex ecosystems the utility of any leading indicator of transitions, including critical slowing down, depends on the region of parameter space over which it is observed. van Nes and Scheffer (2007) showed using numerical techniques that, for several ecological models, critical slowing down occurs far enough from a transition to be a promising indicator of loss of
Fig. 1. Bifurcation diagram and return rate to equilibrium for a predator–prey system (1) with \( f(V) = 1 - V/K, h(V) = 1 - e^{-rV}, r = 0.05, k = 0.05, c = 0.08, f = 10 \). Panels a and b show equilibrium values of the predator population, \( P \), and the prey population, \( V \), as a function of the control parameter, which is the carrying capacity of the prey, \( K \) (note that the parameter \( A \), the predator–prey conversion efficiency, does not affect the equilibrium values). Panels c and d show the return rate to equilibrium (\( \rho \); see text) as a function of the control parameter for \( A = 0.1 \) and 0.5. A transcritical bifurcation occurs at \( K = J \) (see text). A Hopf bifurcation occurs at \( K = K_{crit} = 38.8 \), at which point the stable equilibrium becomes unstable and a stable limit cycle appears. In all panels, the solid lines correspond to stable equilibria; in panels a and b the dashed lines correspond to unstable equilibria and the dotted lines correspond to the upper and lower bounds of the stable limit cycle. The return rate is an increasing function of \( K \) for \( J < K < K_e \) and a decreasing function of \( K \) for \( K > K_e \), where \( K_e = 21.6 \) for \( A = 0.1 \), and \( K_e = 15.7 \) for \( A = 0.5 \).

Fig. 2. Bifurcation diagram and return rate to equilibrium for a Lotka–Volterra competition model (2) with \( a_{12} = 1.4, a_{21} = 1.2, K_2 = 1, r_2 = 1 \). Panels a and b show equilibrium values of the two species’ populations, \( N_1 \) and \( N_2 \), as a function of the control parameter, which is the carrying capacity of species 1, \( K_1 \) (note that the parameter \( r_1 \), the intrinsic rate of increase in species 1, does not affect the equilibrium values). Panels c and d show the return rate to equilibrium (\( \rho \); see text) as a function of the control parameter for \( r_1 = 0.7 \) and 1.3. In all panels, the solid line corresponds to species-1 dominant equilibrium, the dashed line corresponds to the species-2 dominant equilibrium, and the dotted line corresponds to the coexistence equilibrium. The coexistence equilibrium is always unstable for this parameterisation of the model. Saddle-node bifurcations occur at \( K_1 = 0.83 \) and 1.4.
resilience. Here we have provided an analytical treatment of simple two-species models and investigated how the domain over which critical slowing down is observed varies with changes in the models' parameters. But how far from a transition should critical slowing down be observed, or any other leading indicator, occur to be of maximum utility to a manager of a real-world complex system? If the indicator is observed only briefly before a transition, it is unlikely that the transition can be anticipated or avoided. On the other hand, if the indicator is observed over too large a domain of the control parameter, it becomes effectively meaningless as a warning signal. We can suppose that for any given real-world complex system there is an optimal indicator that is intermediate between these two extremes. This optimal indicator would balance the costs of false negatives (i.e., failing to detect an impending transition) against the costs of false positives (i.e., taking action to prevent a transition when none, in fact, is imminent). Thus, the notion of an “optimal” indicator does not really make sense without reference to a specific real-world system and without data on economic costs and benefits. Because of this, the theoretical contributions by us here and van Nes and Scheffer (2007) are only the first steps towards establishing when critical slowing down will be a useful leading indicator of transitions in different ecosystems.

The predator–prey model presented in this paper is a generalisation of previously published predator–prey models (May, 1972; Rosenzweig, 1971). The generalised model has a co-existence equilibrium (6) that exists when the carrying capacity of the prey (our control parameter) is above a certain threshold and is stable when the control parameter is below a second, critical threshold. Above this second threshold, the equilibrium becomes unstable and the model exhibits a stable limit cycle (May, 1972). The tendency for enrichment of a predator–prey system to increase the carrying capacity of the prey and thereby destabilise this system was described as “the paradox of enrichment” by Rosenzweig (1971). Although the transition in the simple deterministic predator–prey model is theoretically reversible, in practice the cyclic behaviour may be undesirable from a management perspective because the oscillations render both species more liable to extinction by stochastic forces. The paradox of enrichment is readily observed in laboratory studies of simple live predator–prey communities (Fussmann et al., 2000, 2005; Roy and Chattopadhyay, 2007), but outside the laboratory the cyclic behaviour is more difficult to observe and may be damped by spatial heterogeneity, the presence of other species in the food web, nutrient recycling and other mechanisms (Nakajima and DeAngelis, 1989; Roy and Chattopadhyay, 2007; Scheffer, 1998).

We can interpret our results for the predator–prey model (1) by observing that there are two forces regulating the growth of the prey population: the first is intrinsic density dependence and the second is predation. When predation is the dominant force the system recovers from perturbations by following a spiral trajectory back towards the equilibrium. Related behaviour is seen in the oscillations of the classic neutrally stable Lotka–Volterra predator–prey model (Roughgarden, 1979). In this regime, critical slowing down is observed as we increase the carrying capacity and move towards the Hopf bifurcation, because increasing the carrying capacity (the control parameter) reduces density dependence, which increases the size of the spiral trajectories, which in turn leads to slower rates of return to equilibrium. By contrast, when intrinsic density dependence is the dominant force, increasing the carrying capacity and thereby strengthening density dependence leads to faster rates of return to equilibrium, and so critical slowing down is not observed. Putting these two observations together we arrive at the
conclusion that critical slowing down on the approach to the Hopf bifurcation is observed over a greater region of control-parameter space in predator–prey models in which predation is stronger and intrinsic density dependence is weaker. This is in accordance with our mathematical results, because weak intrinsic density dependence occurs in models in which the intrinsic rate of increase in prey is low and/or parameters relating to the predator growth rate are high.

The predator–prey model also exhibits another bifurcation: as the carrying capacity is decreased a transcritical bifurcation occurs from the predator–prey coexistence equilibrium to an equilibrium in which the predators are extinct. In terms of critical slowing down, the warning period associated with the transcritical bifurcation decreases exactly as the warning period associated with the Hopf bifurcation increases (Fig. 1). However, the transcritical bifurcation is of less interest to ecologists because it is less likely to be encountered in practice (most ecological systems suffer from excess fertilisation (e.g., Carpenter et al., 1999; Hedin et al., 1995)) and more easily reversed (by nutrient addition). Indeed, most theoretical studies of predator–prey models have focussed on the Hopf bifurcation rather than the transcritical bifurcation (Rosenzweig, 1971 and other studies cited above).

Our competition model is the classic Lotka–Volterra competition model, with the carrying capacity of one species used as the control parameter. In the case with coexistence unstable, the transition from dominance by one species to dominance by the other species is a saddle-node bifurcation and the system exhibits hysteresis. This kind of transition is of particular interest from a management perspective, because the system may exhibit one of two alternative stable states depending on its history. In practice, transitions in hysteretic systems are often difficult or impossible to reverse on timescales relevant to humans (Scheffer and Carpenter, 2003). In the case with coexistence stable, transcritical bifurcations occur between coexistence and dominance by either species.

We can interpret our results for the competition model with coexistence unstable by considering what happens to the two species when the system is perturbed from equilibrium. Let us suppose species 1 is the dominant species and species 2 is the non-dominant species. Near the equilibrium at which species 1 dominates, species 1 is little affected by competition with species 2 and returns to equilibrium at a rate governed almost solely by its own intrinsic rate of increase (this can be shown mathematically for logistic growth). Species 2, on the other hand, is heavily affected by competition and returns to equilibrium at a rate that is dependent on the carrying capacities of the two species. Because only the dynamics of species 2, the non-dominant species, depend on the control parameters (the carrying capacities) critical slowing down will be observed when the dynamics of the system are governed by species 2, in the sense that the eigenvalue corresponding to species 2 determines the rate of return to equilibrium. Thus critical slowing down is observed over a broader region of parameter space when the intrinsic rate of increase in species 2 is slow relative to that of species 1. A similar argument applies to the competition model with coexistence stable, because near a transition one species is always far more abundant than the other (Fig. 3).

We can extend these insights to more complex, multi-species systems and predict that critical slowing down is a better leading indicator of regime shifts triggered by increased resources in multi-species models in which prey species are controlled by predation rather than intrinsic density dependent factors, and in which the dynamics of the rare or non-dominant species operate on timescales that are slower than those on which the dynamics of the common or dominant species operate. Extending our analytical approach to multi-species models would require more sophisticated mathematical techniques than we have used here. Alternatively, our predictions could be tested with multi-species simulation models (e.g., van Nes and Scheffer, 2004) or with real ecosystems.

Examples of ecosystems that have previously been used in studies of regime shifts and could provide such tests are lakes that are enriched by nutrient run-off (Carpenter, 2003; Carpenter and Brock, 2006) aquatic laboratory communities (Fussmann et al., 2000; Fussmann et al., 2005), and rangelands systems (Perrings and Walker, 2004). For instance, imagine a rangeland that is at risk of being overrun by a weed when the grazing pressure (the control parameter) becomes too high. A manager might attempt to detect critical slowing down (and thereby obtain warning of an impending transition) by measuring how the time to extinction of small outbreaks of the weed changes as the grazing rate increases. Our results suggest that this effort to detect critical slowing down is more likely to succeed for weeds that operate on slower timescales than the pasture plants (e.g., woody weeds) than for weeds that operate on timescales similar to the pasture plants (e.g., herbaceous weeds).

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Appendix A. Analysis of equilibria and return rates

A.1. Two-species predator–prey

The Jacobian matrix evaluated at the equilibrium (6) is

\[
\Gamma = \begin{bmatrix}
0 & -h(J) \\
\frac{r^2 f(J)}{kh(J)} & r(\alpha f(J) + Jf'(J))
\end{bmatrix}
\]

(16)

where

\[
\alpha = 1 - \frac{h(J)}{h(J)} > 0
\]

(17)

(which follows from \(h(J)f > h(J)\), which is true because, by assumption, \(h'(J) < 0\)) and

\[
\tau = \frac{\alpha k J}{r} h(J) > 0
\]

(18)

(which follows directly from the assumption \(h'(J) > 0\)).

The equilibrium is stable when the determinant of \(\Gamma\) is positive and the trace is negative (these are the Routh–Hurwitz criteria for a \(2 \times 2\) continuous-time system), which occurs when \(\alpha f(J) + Jf'(J) < 0\). The derivative of the left hand side of this expression with respect to \(K\) is positive; so as \(K\), the control parameter, increases, the equilibrium becomes unstable and the critical transition to a Hopf bifurcation occurs at some value of \(K = K_{\text{crit}}\), where

\[
\alpha f(J) + Jf'(J) = 0
\]

(19)

To find the recovery rate (assuming the equilibrium is stable) we compute the eigenvalues of \(\Gamma\) and find the dominant
eigenvalue:
\[ \rho = |\lambda_{dom}| = -\lambda_{dom} = \begin{cases} \frac{-\delta/2,}{\delta^2 + 4\beta\gamma > 0} \\ \frac{-\delta - \sqrt{\delta^2 + 4\beta\gamma}}{2}, \quad \delta^2 + 4\beta\gamma < 0 \end{cases} \]

where
\[ \beta = -kh(J) \]
\[ \gamma = \frac{\gamma_1 f(J)}{kh(J)} \]
\[ \delta = \frac{r(2f(J) + Jf'(J))}{C_0} \]

By taking the derivative of \( \rho \) with respect to the control parameter, \( K \), we find that recovery rate decreases for \( \delta^2 + 4\beta\gamma < 0 \) and increases for \( \delta^2 + 4\beta\gamma > 0 \). Therefore, the maximum recovery rate occurs for some value of \( K = K_r \) when \( \delta^2 + 4\beta\gamma = 0 \), which occurs when
\[ 2f(J) + Jf'(J) = 2\sqrt{rf(J)} \]

A.2. Two-species competition (coexistence unstable)

We investigate the transition from the equilibrium (10) at which species 1 is dominant to the equilibrium (11) at which species 2 is dominant. The Jacobian at equilibrium (10) is
\[ \Gamma = \begin{bmatrix} -r_1 & 0 \\ -r_2 \xi_{12} & -r_2(2\xi_1 K_1/K_2 - 1) \end{bmatrix} \]

The eigenvalues of the Jacobian are
\[ \lambda_1 = -r_1 \]
\[ \lambda_2 = -r_2(2\xi_1 K_1/K_2 - 1) \]

and so the recovery rate is
\[ \rho = |\lambda_{dom}| = \min(r_1, r_2(2\xi_1 K_1/K_2 - 1)) \]

The recovery rate is constant \( \rho = r_1 \) with respect to the control parameter, \( K \), for \( r_1 < r_2(2\xi_1 K_1/K_2 - 1) \). As the control parameter increases, the recovery rate begins to decline where the two eigenvalues are equal, which occurs at
\[ K_1 = K_r = \left( 1 + \frac{r_1}{r_2} \right) \frac{K_2}{2\xi_1} \]

A.3. Two-species competition (coexistence stable)

We investigate the transition from coexistence to dominance by one of the species. The Jacobian at the coexistence equilibrium is
\[ \Gamma = \begin{bmatrix} -\beta & -2\xi_1 \gamma \\ -2\beta \xi_1 & -\gamma \end{bmatrix} \]

where \( \beta = r_1 \xi_1/K_1 \) and \( \gamma = r_2 \xi_2/K_2 \). It is easily shown that the conditions for stability of the coexistence equilibrium are the same as the conditions for its existence. The criterion for coexistence is \( \xi_1\xi_2K_1 < 1 \) from which it follows that
\[ (\beta + \gamma)^2 > 4 \det \Gamma = 4\beta\gamma(1 - \xi_1\xi_2K_1) \]

When \( \xi_1 \) and \( \xi_2 \) are not too small (i.e., their product is sufficiently close to one), we can make the stronger assumption that
\[ (\beta + \gamma)^2 > 4 \det \Gamma = 4\beta\gamma(1 - \xi_1\xi_2K_1) \]

and that the eigenvalues are given by the approximations
\[ \lambda_1 \approx -\beta - \gamma \]
\[ \lambda_2 \approx \frac{\beta\gamma(1 - \xi_1\xi_2K_1)}{-\beta - \gamma} \]

Under this approximation, the magnitude of \( \lambda_2 \) is greater than that of \( \lambda_1 \), so the recovery rate is approximated by
\[ \rho = |\lambda_{dom}| = -\lambda_2 \approx \frac{\beta\gamma(1 - \xi_1\xi_2K_1)}{-\beta + \gamma} \]

which has its maximum with respect to the control parameter, \( K \), at
\[ K_1 = K_r = \frac{\sqrt{r_1}}{r_1^2 \xi_1 K_1 + 1} \]

References


