**Ecological resilience of population cycles:
a dynamic perspective of regime shift**

Kenta Suzuki* and Takehito Yoshida

Department of General Systems Studies, Graduate School of Arts and
Sciences, University of Tokyo, 3-8-1 Komaba, Tokyo, 153-8902, Japan

* Present address: Center for Environmental Biology and Ecosystem Studies,
National Institute for Environmental Studies

Corresponding author: Kenta Suzuki, suzuki.kenta@nies.go.jp

Abstract

Studies of catastrophic regime shifts have mostly considered a simple equilibrium situation, in which there are two stable equilibria divided by an unstable equilibrium. However, populations and communities in nature often show more complex dynamics, and regime shifts in the complex dynamic systems have attracted limited attention so far. Understanding the division between alternative stable states in multispecies communities requires an extended perspective and the conventional analysis of a simple equilibrium situation cannot be applied as it is. What divides the alternative stable states can take complex structure rather than a point, and this division of alternative states is usually impossible to be obtained by analytical approaches. In this study, we developed a numerical method that can relatively easily provide the structure of the division of alternative stable states. We then applied the method to different three-species systems exhibiting oscillatory dynamics to understand their recoverability from perturbations that can bring out irreversible state change. Our results suggested that there is temporal variation of the recoverability that may not be understood straightforwardly because of the complex structure of the division of alternative stable states. Also, which of the alternative states is more vulnerable to perturbations and easier to show a regime shift can vary depending on the size of perturbation. These attributes of regime shifts have not been found in a simple equilibrium situation, suggesting the need of a dynamic aspect of the recoverability of ecological systems.

Keywords

catastrophic regime shifts, alternative stable states, basin boundary, food web, population dynamics

1. Introduction

In ecological systems with alternative stable states (ASS, hereafter), there are possibilities of regime shifts by two different mechanisms (Scheffer et al. 2001, Scheffer and Carpenter 2003). One is the gradual shift of parameters that can alter the stability of stable states (attractors). In recent years, this mechanism has been extensively studied in the attempts to find early warning signals for the catastrophic regime shifts accompanied with gradual environmental changes (Carpenter and Brock 2006, Carpenter et al. 2008, Dakos et al. 2008, Guttal and Jayaprakash 2008, Scheffer et al. 2009, Carpenter et al. 2011). Another mechanism is due to the perturbations that can bring the state of a system into the basin of attraction of a different stable state and thus trigger a regime shift (Scheffer and Carpenter 2003). In this study, we focus on this mechanism by analyzing the recoverability of ecological systems from perturbations. Such recoverability has been acknowledged in the definition of “ecological resilience” (Holling 1996, Gunderson 2000) that measures the size of perturbation, against which the system can hold its original state. However, this mechanism has been seen largely conceptual and the practical description based on theoretical consideration is still lacking.

Ecological resilience is usually explained by a double potential well (Fig. 1a, e.g. Holling 1996, Scheffer et al. 2001, Scheffer and Carpenter 2003). There are two potential minima and one maximum that correspond to stable states (stable equilibria) and a division of the basins of attraction (unstable equilibrium), respectively. This picture intuitively explains ecological resilience as the distance from a stable equilibrium to an unstable equilibrium. However, this conventional description lacks two important features of the recoverability of ecological systems (Fig. 1b). First, when a system contains more than two species, the division of alternative states is no longer a simple tipping “point” but a manifold that often takes a complex structure. Second, the stable state may not be an equilibrium but can be intrinsic fluctuations. In the dynamic system theory, a division of alternative states corresponds to a basin boundary (boundary of the basins of attraction), and the relationship between stable states and the basin boundary can be shown in a phase space whose axes are population densities of species included in the system. Besides the special case in which basin boundary is a point, it is usually impossible to obtain the basin boundary as an analytical

79 solution of a dynamic system, although it provides essential knowledge on
80 the recoverability of the stable states.

81 Theoretical studies have predicted ASS in ecological systems since
82 the 1960s (Lewontin 1969, Holling 1973, May 1977), and the existence of
83 ASS has been suspected in a wide range of natural systems [marine systems,
84 Petraitis and Dudgeon (2004), Daskalov et al. (2007); lakes and ponds,
85 Cottenie et al. (2001), Carpenter et al. (2011); rivers, Dent et al. (2002);
86 terrestrial systems, McCune and Allen (1985), Ripple and Beschta (2006)].
87 However, empirical findings obtained from non-experimental approaches
88 offer only indirect evidence of ASS and are still open for alternative
89 explanations. In contrast, manipulation experiments provide direct evidence
90 for the presence or absence of ASS. Schröder et al. (2005) reviewed 35
91 manipulative experiments and found that 13 of them showed clear evidence
92 for ASS, whereas 8 demonstrated the absence of ASS (14 studies were not
93 appropriate tests for ASS in their criteria). More importantly, stable states
94 in the five experiments showing ASS included population fluctuations. Based
95 on this finding, they insisted that “it is not surprising that ASS can also
96 contrast in the type of their intrinsic dynamics” (e.g., Murdoch 2002, De Roos
97 and Persson 2003, Wearing et al. 2004, McCauley et al. 1999, Henson et al.
98 2002, Zamamiriet al. 2001), although “ASS are still often perceived as
99 contrasting equilibrium values where a system exhibits fix-point stability in
100 each of its states” (e.g., Beisner et al. 2003).

101 In the present study, based on the “straddle orbit” (Battelino et al.
102 1988, Grebogi et al. 1988), a method to approximate the structure of basin
103 boundary was developed. In the different types of ecological system
104 consisting of three species, we used the approximated basin boundary to
105 investigate the properties of regime shifts that have not been considered in
106 the previous studies. At first, we focused on the temporal change of the
107 recoverability associated with the population fluctuation. For this purpose,
108 we quantified the time dependency of the distance to basin boundary based
109 on our approximation (Fig. 1d). We then evaluated the responses to
110 perturbations with variable magnitudes and compared them between the
111 alternative states (Fig. 1f). The properties of recoverability predicted in this
112 study were quite different from those in the case of two stable equilibria and
113 an unstable equilibrium studied in the majority of the relevant literature
114 (Fig. 1c, e).

2. Methods

2.1 Approximation of basin boundary

Time development of an ecological system corresponds to a trajectory in a phase space. Our method to obtain the structure of basin boundary is based on the knowledge that there are trajectories lying along the boundary. Battelino et al. (1988) proposed the straddle orbit method, by which such trajectories are tracked. Although one trajectory provides only a little information, the union of many trajectories provides a good approximation of the basin boundary (see Appendix A for more detailed description of our method). We define the approximated basin boundary as β (Eq. A.2).

2.2 Definition of local ecological resilience and vulnerability index

Using the approximated basin boundary β , one can evaluate when the system is sensitive to external perturbations and shows a regime shift to another stable state. Here, we define “local ecological resilience (LER)” of a stable state i as follows,

$$LER_i(t) = \min(\{d(\mu_i(t), y) | y \in \beta\}), \quad (1)$$

where $\mu_i(t)$ is a state vector of a trajectory at time t , and $d(\mu_i(t), y)$ is the Euclidean distance between the state vector and that of approximated basin boundary y in a phase space. Equation 1 defines LER as the minimum distance from the stable state to the basin boundary at each time. Therefore, one can expect that the system easily changes its state in response to a perturbation when LER is small. Note that the original idea of ecological resilience and LER we defined are different. As mentioned above, ecological resilience can be measured as the size of perturbations, against which the system can hold its original state (Holling1996, Gunderson 2000). However, the recoverability of the system would be different depending on the position in the stable state (Fig. 1d). Thus, there is temporal variation of the recoverability in the bistability of cyclic dynamics, although it is constant if we consider the bistability of equilibrium (Fig. 1c). For the oscillatory dynamics, LER is more suitable for estimating how a state of an ecological system is sensitive to perturbations.

LER evaluated for alternative states are generally non-identical because of the difference in their relationship to the basin boundary in the

phase space. The difference of LER between alternative states implies that the occurrence of regime shifts differs among alternative states. More importantly, depending on the perturbation size, alternative states can have a different contrast in the recoverability of the system (Fig. 1f). To quantify this, we define vulnerability index (VI) of a stable state i as a function of perturbation size,

$$VI_i(L) = \lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T \frac{\theta(L - LER_i(t))}{L} dt, \quad (2)$$

$$\theta(x) = \begin{cases} x & \text{if } x > 0 \\ 0 & \text{if } x \leq 0 \end{cases}. \quad (3)$$

$VI_i(L)$ evaluates how frequently the perturbations whose norm is equal to L exceed LER along with the trajectory of a stable state i . If VI of i is larger than that of another stable state j at a certain perturbation size, stable state i is more vulnerable than stable state j in the sense that the transition from i to j occurs more easily than vice versa. This results in that stable state i has a larger transition rate than stable state j in the numerical experiment described below. $VI_i(L)$ should be defined as the average for the infinitely long time interval T because a state of the system can be non-periodic dynamics such as chaos. Practically, T is selected so that it is sufficiently larger than the time scale of population dynamics.

The increase of VI along with the perturbation size is basically common to any bistable systems (Fig. 1e, f), whereas it can take various patterns in bistable systems with non-point basin boundary. For example, in Figure 1f, the VI of one attractor (indicated by black point) is larger than that of the other (indicated by gray point) when perturbation size is small (indicated by small circles). On the other hand, when perturbation size is large (indicated by large circles), the vulnerabilities of the two attractors have the reversed contrast, resulting from the complicated shape of the basin boundary. VI is defined so as to quantify such effects of a basin boundary regardless of the dynamics of stable states.

179

180 2.3 Numerical perturbation experiment

To confirm that LER and VI actually indicate the vulnerability of the stable states against perturbation, we calculated the transition rate to the alternative state in a numerical perturbation experiment; in a sufficiently large number of trials (100 simulation trials), a perturbation vector whose

norm did not exceed σ_m was added to a state vector of the system at time t (i.e., in each trial the system is perturbed only once), and after taking the absolute value to avoid negative population density, whether it induced the transition to alternative state or not was checked to calculate the transition rate at t for the perturbation size σ_m . Thus, we assumed the uniform distribution as the perturbation kernel for our numerical experiment, although it can be different in natural conditions. The result of this numerical experiment should be consistent as long as a perturbation kernel that has a mean of zero and symmetrical distribution around the mean is used. The transition rate is expected to be high when LER is low because low LER indicates that the basin boundary lies close to the attractor trajectory.

2.4 Model description

As an example of regime shifts of alternative cyclic dynamics, differential equation models consisting of three species were examined. In three-species models, the bifurcation structure, which shows the type and the numbers of stable states in parameter space, has been intensively studied in the past few decades (see below for the details). These previous studies were helpful in finding the parameter combination, with which the system has alternative cyclic dynamics. In all of the models used here, the logistic growth of the basal species and the Holling type II functional response were assumed.

Model 1: One-predator-two-prey model

The one-predator-two-prey model is described by the following equations:

$$\frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1 + c_{12} x_2}{K_1}\right) - b_{12} x_1 x_2 - \frac{\epsilon a_1 x_1 y}{k + x_1 + x_2}, \quad (4)$$

$$\frac{dx_2}{dt} = r_2 x_2 \left(1 - \frac{x_2 + c_{21} x_1}{K_2}\right) - b_{21} x_2 x_1 - \frac{\epsilon a_2 x_2 y}{k + x_1 + x_2}, \quad (5)$$

$$\frac{dy}{dt} = \frac{\sum_{i=1,2} a_i x_i y}{k + x_1 + x_2} - d y. \quad (6)$$

Here, x_1 and x_2 represent the population densities of prey 1 and prey 2, respectively, and y represents that of the predator. r_i is the growth rate and K_i is the carrying capacity of prey i . c_{ij} represents the effect of exploitative competition of prey j on prey i , and b_{ij} represents the effect of interference competition of prey j on prey i . a_i is the predation rate for prey i , k is the half saturation density, d is the mortality rate of the predator, and ϵ is the

reciprocal of the conversion efficiency. We assumed that prey 1 is a superior competitor for resource exploitation compared to prey 2 ($r_1 > r_2$, $K_1 > K_2$, $c_{12} < c_{21}$), whereas prey 2 is more defended against the predator ($a_1 > a_2$) and a superior competitor for interference competition ($b_{12} > b_{21}$) compared to prey 1. This tradeoff can give rise to bistability in this system.

The one-predator-two-prey model was first studied to demonstrate the existence of chaotic solutions with particular parameter values (Gilpin 1979), and then followed by other numerical studies that provided more detailed results of its dynamics (Schaffer and Kot 1985, Schnabl et al. 1991). Then, using bifurcation analysis based on normal form (the simplest form of the differential equation used in bifurcation analysis that provides information about what kind of bifurcation can occur in the model at a certain point of the parameter space), the existence of saddle-node, transcritical and Hopf bifurcations of limit cycles, which can bring about bistabilities including non-point dynamics, was revealed (Klebanoff and Hastings 1994a). This conclusion is basically independent of the particular type of model (e.g., type of functional response) and parameter values, because these model variants can be transformed to the same normal form. Furthermore, even three-species food chains can also be transformed to the same normal form (Klebanoff and Hastings 1994a). Therefore, the result also applies to the three-species food chain model described below.

Model 2: Food-chain model

The three-species food chain model is described by the following equations:

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) - \frac{\epsilon_1 a_1 xy}{k_1 + x}, \quad (7)$$

$$\frac{dy}{dt} = \frac{a_1 xy}{k_1 + x} - \frac{\epsilon_2 a_2 yz}{k_2 + y} - d_2 y, \quad (8)$$

$$\frac{dz}{dt} = \frac{a_2 yz}{k_2 + y} - d_3 z. \quad (9)$$

Here, x , y and z represent the population densities of the basal species, first consumer, and top predator, respectively. r is the growth rate and K is the carrying capacity of the basal species. a_i is the predation rate, k_i is the half saturation density for the predation from trophic level $i + 1$ to i , d_i is the mortality rate of trophic level i , and ϵ_i is the reciprocal of the conversion efficiency.

For three-species food chain models, previous simulation studies showed the period doubling routes to chaos (Hastings and Powell 1991, McCann and Yodzis 1995), which was more deeply studied by the bifurcation analysis (Klebanoff and Hastings 1994b, Kuznetsov and Rinaldi 1996). As we already mentioned, the normal form of the three-species food chain and two-predator-one-prey system is the same (Klebanoff and Hastings 1994a). Therefore, bifurcations can also bring about alternative cyclic dynamics in this model.

Model 3: Two-predator-one-prey model

The two-predator-one-prey model is described by the following equations:

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) - \sum_{i=1,2} \frac{\epsilon a_i xy_i}{k_i + x}, \quad (10)$$

$$\frac{dy_1}{dr} = \frac{a_1 xy}{k_1 + x} - b_{12} y_1 y_2 - d_1 y_1, \quad (11)$$

$$\frac{dy_2}{dr} = \frac{a_2 xy}{k_2 + x} - b_{21} y_2 y_1 - d_2 y_2. \quad (12)$$

Here, x is the population density of prey, and y_1 and y_2 are those of the two competing predators, predator 1 and 2, respectively. r represents the per capita growth rate, and K is the carrying capacity of prey. a_i is the predation rate, k_i is the half saturation density for each of the predators and ϵ is the reciprocal of the conversion efficiency. b_{ij} represents the competitive effect of predator j on predator i (interference between predators), and d_i is the mortality rate of the predators. We assumed that predator 1 is a weak competitor compared to predator 2 in terms of both exploitative and interference competition ($k_1 = k_2, a_1 < a_2$ and $b_{12} > b_{21}$), whereas the mortality of predator 1 is smaller than that of predator 2 ($d_1 < d_2$). This tradeoff between competitive ability and mortality guarantees that one of the predators is not always superior to the other, which can give rise to bistability in this system..

There are many studies on the dynamics of a two-predator-one-prey system (e.g. Hsu et al. 1978, Koch 1978, Vance 1978, Smith 1985, Muratori and Rinaldi 1989), but most of these previous studies assumed that there is no interference competition between predators, i.e., $b_{12} = b_{21} = 0$. On the other hand, Vance (1978) showed that there are bistabilities of limit cycles in the model with interference competition $b_{12} = b_{21} \neq 0$. The main scope of

these previous studies was to show the condition in which two competing predators can coexist, but not the bistability of the system.

2.5 Simulation of the model

We used Mathematica (version 10) to solve differential equations and implement algorithms. Sample codes for our algorithms are given as a supplementary material (S1).

3. Results

3.1 Temporal variation of local ecological resilience

The one-predator-two-prey system has bistability of three-species chaos (indicated by the largest Lyapunov exponent calculated by the algorithm of Shimada and Nagashima (1979)) and equilibrium only with prey 2 (Fig. 2a, 3a and b; see also Appendix B). The basin boundary between the two attractors is approximated as a smooth plane (Fig. 2b, c). Local ecological resilience (LER) of three-species chaos shows clear temporal fluctuations (Fig. 3c), although that of the equilibrium is constant (Fig. 3d). The result of the perturbation experiment for the chaotic attractor (Fig. 3e) showed the good correspondence between low LER and high transition rate to a different state, while the transition rate tended to be constant for the equilibrium (Fig. 3f). Therefore, LER effectively indicated when the system is sensitive to external perturbation and prone to show a regime shift. It is worth noting the relationship between population dynamics (Fig. 3a) and LER (Fig. 3c). In the three-species chaos, LER approaches its local minima when the prey 2 density is smaller than that of prey 1 and the prey 2 density approaches its local minima. This is counterintuitive because the alternative equilibrium only consists of prey 2, and thus the low density of prey 2 in the chaotic attractor seems quite far from the alternative attractor of equilibrium in the phase space. However, the local minima of prey 2 actually correspond to the local maxima of the predator, at which the chaotic attractor approaches to the basin boundary (Fig. 2c, 3a and b). Thus, depending on the configuration of the stable states and the basin boundary, this system can show the unexpected transition to a different stable state as well as the temporal fluctuations of the recoverability.

The three-species food chain model has bistability of two different types of three-species limit cycles contrasting in their amplitudes (Fig. 4a, 5a and b; see also Appendix B). The good correspondence between LER and the transition rate was also confirmed (Fig. 5c, d, and e, f). The two attractors share the same characteristic that LER is in the lowest level when the population density of the first consumer is low (Fig 5a, b and c, d). What is important here is that the basin boundary has a complicated structure, although the stable states of the system are limit cycles (Fig. 4a-c). This means that even in the cases that we observe simple oscillations of population densities, it may not necessarily mean that the fluctuation of LER also has the similar pattern of simple oscillations. Thus, the relationship between population dynamics and LER is not clear compared to the former case of the one-predator-two-prey system. There are experimental findings that indeed showed alternatively stable oscillatory dynamics with different amplitudes (e.g. Jilson 1999, McCauley et al. 1999, McCauley et al. 2008), although as for the three-species food chain model we considered here, the bistability of the two types of three-species limit cycles rarely occur within the parameter space.

The two-predator-one-prey system has large parameter space where the two predators are mutually exclusive if, as we assumed in our model, the predators have a tradeoff between competitive ability and mortality. As a result, the coexistence of two types of two-species (predator-prey) limit cycles occurs (Fig. 6a, 7a and b; see also Appendix B). The phase space is divided into two parts, each of which corresponds to the basin of each two-species limit cycle, and the basin boundary of this system is a plane embedded in the phase space (Fig. 6b, c). The correspondence between LER and the transition rate was also confirmed (Fig. 7c, d and e, f). In both of the limit cycles, LER is in the lowest level when the predator density declines to local minima and prey density starts to increase (Fig. 7a, b and c, d), which correspond to where the distance between the limit cycles approaches its local minima in the phase space.

3.2 LER and asymmetric responses to perturbations

LER is not identical between the alternative states (Fig. 3c, d, 5c, d and 7c, d), suggesting that one stable state is predominant over the other if perturbations frequently cause the transition between them. Moreover,

which stable state becomes predominant depends on the size of perturbation and it can be reversed in some cases. The transition from one stable state to the other can be characterized by the vulnerability index (VI) as defined above, and indeed, VI corresponds well with the results of the numerical perturbation experiment (Fig. 8).

The VIs of the one-predator-two-prey model and the two-predator-one-prey model show similar responses to different perturbation size (Fig. 8a, e). However, in the one-predator-two-prey model, there is an immediate increase of VI at the small perturbation size only in the chaotic attractor (Fig. 8a). This is because the chaotic attractor and its basin boundary are close in some part of the phase space, while the alternative state of equilibrium is apart from the basin boundary. Even when perturbation size exceeds LER, the transition rate does not increase as in VI (Fig. 8b). This is because the basin boundary inclines away from the equilibria, and VI is estimated based on the minimum distance to the basin boundary. In the two-predator-one-prey model, VIs and the transition rates of the stable states diverge at first and then converge to a similar level (Fig. 8e, f). The three-species food chain model showed the interesting result that the VIs of the two limit cycles are reversed at a certain perturbation size (Fig. 8c), which is also observed in the transition rate (Fig. 8d). It is important to mention again that this variety of responses to perturbations with different size arises because of the configuration of stable states and basin boundary in the phase space as shown in Fig. 2, 4 and 6, and these diverse patterns appear only when we consider the alternative stable states with non-point basin boundary.

4. Discussion

The recoverability of the three-species systems we studied showed remarkable temporal fluctuation, suggesting that perturbations can trigger regime shift at some time point but not at the other. This dynamic view of regime shifts results from the consideration of oscillatory dynamics, but it has been overlooked in the previous studies of regime shifts that mostly focused on equilibria (e.g., Scheffer et al. 2001, Scheffer and Carpenter 2003). Because natural systems often show oscillatory dynamics (Murdoch et al. 2002, Ives and Carpenter 2007), regime shifts needs to be considered in the

dynamic framework, although a good understanding of the stable states and the basin boundary, which is necessary to predict when the regime shift occurs, is often difficult in natural systems. Nevertheless, our study showed that the temporal variation of recoverability could be quantified using LER if we knew the dynamic structure governing a system (Fig. 3c, d, 4c, d and 5c, d). The recoverability of ecological systems may not be simply determined by the population dynamics, it is indeed determined by the configuration of the stable states and the basin boundary in the phase space (Fig. 2b, 4b and 6b), and it naturally and implicitly involves temporal variations due to the oscillatory nature of population dynamics (Schröder et al. 2005).

In addition to the temporal variation, the structure of basin boundaries also influences how vulnerable each stable state is against perturbations with different size. Although alternative equilibria associated with an unstable equilibrium always show the same contrast of the vulnerability over the range of perturbation size (Fig. 1e), the vulnerabilities of three species dynamics we studied have various patterns depending on the configurations of the stable states and the basin boundary (Fig. 2, 4, 6 and 8). The alternative stable states with non-point basin boundary may have similar or different vulnerability against perturbation depending on the perturbation size, and which dynamics is more vulnerable against perturbation than the other can be reversed depending on the size of perturbation, as the vulnerability index (VI) suggested (Fig. 8). This implies that one can observe the regime shift from an alternative state A to the other state B more frequently than that from B to A at a certain size of perturbation, but this propensity can be reversed at a different size of perturbation so that the regime shift from B to A happens more frequently. Thus, depending on the size of perturbation, regime shifts can be very different in a system having the non-point basin boundary structure.

It should be mentioned that LER and VI indicate the maximum expectation of the vulnerability to perturbations because both indices are calculated using the minimum distance to basin boundary. Thus, considering that the effect of perturbation depends not only on its size but also on its direction, LER and VI can overestimate the vulnerability if the distance to basin boundary is highly variable depending on the direction of perturbation. In this study, most of the results were not affected by this dependency on the direction of perturbation, except for the result showing the mismatch

between VI and the transition rate calculated in the numerical experiment (Fig 8a, b).

Our results can also be discussed in the context of the invasibility of ecological communities. Recently, Yamamichi et al. (2014) suggested that the invasibility of a community changes depending on the timing of invasion in relation to the intrinsic population cycles as well as the size of invader population (propagule pressure). As the transition from a community with a less number of species to another with more species indicates the invasion of new species, our results showing the temporal changes of LER support the argument of Yamamichi et al. (2014). As they showed, this property of the invasibility depends on the structure of the basin boundary that separates the basin of a native community and that of an invaded community. Thus, our method for approximating the basin boundary can be used to deepen the understanding of invasibility as well.

Some of the recent studies reported that there are leading indicators of regime shifts (Carpenter and Brock 2006, Carpenter et al. 2008, Dakos et al. 2008, Guttal and Jayaprakash 2008, Scheffer et al. 2009, Carpenter et al. 2011). As we already mentioned, these previous studies considered the gradual shifts of environmental conditions as the mechanism that triggers regime shifts. One of the merits of this approach is that it requires only the time series data to calculate the statistical leading indicators (variance, autocorrelation, skewness etc.). However, the leading indicators so far apply to the systems whose underlying stable states are equilibria, and regime shifts in cyclic and chaotic systems are less studied with regard to the leading indicators (Scheffer et al. 2009). Generally speaking, leading indicators exist when engineering resilience (the reciprocal of the return time to a stable state) smoothly declines as a certain parameter shifts toward a critical point. In contrast, the existence of leading indicators is not obvious in the systems that exhibit complex dynamics because these systems generally possess non-smooth potential, with which the smooth change of engineering resilience is not expected (Hastings and Wysham 2010). Thus, although the leading indicators can be calculated for the systems showing complex dynamics, there are limitations due to the dynamic properties.

In contrast, we considered in this study the regime shifts that are triggered by perturbations. In order to predict the regime shifts, our method requires the basic equations structuring the system to be known, although

tremendous difficulties exist in modeling complex ecological systems. However, the recent progress in meta-genomics starts to provide large data sets that can be used to model multispecies dynamics including their responses to perturbations (Stein et al. 2013). We expect that such the methodological progress extends the possibility of application of our approach.

In conclusion, we demonstrated that the recoverability of complex ecological system cannot be understood by the conventional concept of a regime shift between alternative equilibria associated with an unstable equilibrium. The dynamic aspect of a regime shift comes from the configuration of stable states and basin boundaries in a phase space. We believe that our attempt is an important step in understanding regime shifts in natural ecosystems that show diverse behavior of population dynamics. We studied the recoverability of three-species systems, which are the smallest systems showing bistability of oscillatory dynamics. The properties of ecological systems with many interacting species (van Nes and Scheffer 2004) remain to be studied, for example, to find out the characteristics of species that make them a more sensitive trigger of a regime shift than others.

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Appendix A: Straddle orbit method and approximation of basin boundary

The straddle orbit method (below) was proposed to obtain a saddle orbit laying on an unstable manifold (i.e., basin boundary). Because the saddle orbit is stable only on the unstable manifold, this can be an attractor of the system restricted on the unstable manifold. One can effectively track the trajectory on this unstable manifold by taking two points in the different sides of the manifold and keeping the distance of these points below a certain level along with the trajectory. This pair of trajectories theoretically converges to the saddle orbit (or saddle point) on the unstable manifold. Here, we define a pair of trajectories obtained from the straddle orbit method as,

$$\Phi_i(t) = (\varphi(x_{0i}, t), \varphi(y_{0i}, t)) \quad (\text{A.1})$$

where, x_{0i} and y_{0i} is the initial value belongs to the different basin of attraction and $\varphi(x, t)$ is the state vector of a trajectory initiates from x at time t . As its definition, $d(\varphi(x_0, t), \varphi(y_0, t)) < \delta$. Here, $d(\cdot)$ is the Euclidean distance between the state vectors and δ is a small positive real number. Then, we consider a union of the mean of these trajectories as the set of points approximating a basin boundary:

$$\beta = \bigcup_{i \in I} \tilde{\Phi}_i(t) \quad (\text{A.2})$$

where,

$$\tilde{\Phi}_i(t) = \frac{\varphi(x_{0i}, t) + \varphi(y_{0i}, t)}{2} \quad (\text{A.3})$$

The same method was used in order to visualize the structure of basin boundaries (Engbert and Drepper 1994, Tedeschini-Lalli 1995), although the present study is the first one that applies this method to the understanding of ecological resilience.

Straddle Orbit Method (Battelino et al. 1988)

1. Choose two points that belong to the basin of two different attractors: say point P_A goes to the attractor A , and P_B goes to the attractor B .
2. Bisect the segment P_AP_B and set the middle point as P_C
3. Determine which basin of attraction P_C belongs to. If P_C is in the basin of the attractor A , replace P_A by P_C and set P_C as new P_A , thus giving a new segment P_AP_B that is half as far apart as before.

- 645 4. Go back to step 2 and keep repeating the procedure (given by steps 2 and
646 3) until the length of the segment P_AP_B is less than a small predetermined
647 value δ (10^{-8}).
- 648 5. Repeat the numerical integrations initiate from the points P_A and P_B , and
649 at every time step, check if the length of the segment P_AP_B is greater than δ .
650 If it is, repeat steps 2 and 3 until the distance P_AP_B again becomes less than
651 δ .
- 652 6. Repeat step 5 for a large number of time steps (10,000) and plot P_A or P_B .

Appendix B: Bifurcation analysis for the three-species models

Figure B.1 is the bifurcation diagram of the one-predator-two-prey model we studied. The system is bistable between b_{12} values indicated by the arrows. The chaotic attractor appears through period doubling bifurcation and it suddenly disappears due to a boundary crisis with the further increase of b_{12} , making the equilibrium globally stable. In contrast, the equilibrium becomes unstable with the decrease of b_{12} due to a transcritical bifurcation and the equilibrium or limit cycle that is on the branch from the chaotic attractor becomes globally stable.

Figure B.2 is the bifurcation diagram of the three-species food chain we studied. The system is bistable between a_1 values indicated by the arrows. The figure shows that the large-amplitude limit cycle disappears due to a saddle-node bifurcation as a_1 and a_2 increase, and the small-amplitude limit cycle becomes globally stable. In contrast, the small-amplitude limit cycle disappears also due to a saddle-node bifurcation as a_1 decreases and the large-amplitude limit cycle becomes globally stable (except for panel f).

Figure B.3 is the bifurcation diagram of the two-predator one-prey model we studied. The system is bistable between b_{12} values indicated by the arrows. The limit cycle with predator 2 and prey becomes unstable with the increase of b_{12} due to a transcritical bifurcation where the limit cycle collides with an unstable periodic orbit with three-species, and the further increase of b_{12} results in the globally stable limit cycle with predator 1 and prey. In contrast, the limit cycle with predator 1 and prey becomes unstable due to a transcritical bifurcation with the decrease of b_{12} where the limit cycle in turn collides with the unstable periodic orbit, and then the limit cycle with predator 2 and prey becomes globally stable with the further decrease of b_{12} .

Figure legends

Figure 1. The difference between stability of equilibrial states divided by an unstable equilibrium and that of oscillatory dynamics divided by a basin boundary. (a) A potential description explaining ecological resilience. Solid line describes the stability of equilibria. Dotted line indicates the position of tipping point (unstable equilibria) that corresponds to the basin boundary between the two stable equilibria. (b) A diagram describing the phase space of a system that has two species and cyclic dynamics. Stable states are indicated by solid loops (limit cycles) and are divided by a curve (dotted line) that is the basin boundary. Distance to the basin boundary (see our definition of LER in section 2.2) is constant in the bistability of equilibria (c), whereas there is temporal variation in the bistability of cyclic dynamics (d, indicated by the different lengths of arrows). In bistability with an unstable equilibrium, the vulnerability of stable states (see our definition of VI in section 2.2) increases with the perturbation size, and it shows the same contrast between the stable states over the range of perturbation size (e). In a system with the non-point basin boundary, however, the increase of the vulnerability with the perturbation size can take various patterns depending on the boundary structure (f, circles indicate perturbations having the same size). For simplicity, we described the stable states as a point equilibrium in (f).

Figure 2. Phase space plot of the two attractors and the result of basin boundary analysis for the one-predator two-prey model. (a) Chaos and an equilibrium shown in a three-dimensional phase space (blue: three-species chaos, green: equilibrium with prey 2). (b) Basin boundary between the two attractors approximated by 250 trajectories obtained from the straddle orbit method (shown in red). (c) Basins for chaotic attractor (light gray) and equilibrium (dark gray) in the 2D plane shown in (b). Intersections with the trajectories of the chaotic attractor (blue points) and that of basin boundary (red points) are indicated. The parameter values are, $K_1 = 0.63, K_2 = 0.37, k = 0.5, r_1 = 1, r_2 = 0.45, d = -0.2, a_1 = 1.85, a_2 = 0.14, b_{12} = 2.9, b_{21} = 0.33, c_{12} = 0.25, c_{21} = 1.63$ and $\epsilon = 2$.

Figure 3. LER and the result of numerical perturbation experiment for the one-predator two-prey model. (a) Population dynamics of the three-species

chaos (black line: prey 1, gray line: prey 2, dotted line: predator), the corresponding LER (c) and the transition rate (e) in the numerical perturbation experiment (100 simulation trials, $\sigma_m = 0.03$). (b) Population dynamics of the equilibrium (black line: prey 1, gray line: prey 2), the corresponding LER (d) and the transition rate (f) in the numerical perturbation experiment.

Figure 4. Phase space plot of the two attractors and the result of basin boundary analysis for the three-species food chain model. (a) Two limit cycles in a three-dimensional phase space (blue: low-amplitude cycle, green: high-amplitude cycle). (b) Basin boundary between the two limit cycles approximated by 250 trajectories obtained from the straddle orbit method (shown in red). (c) Basins for low-amplitude cycle (light gray) and high-amplitude cycle (dark gray) in the 2D plane shown in (b). Intersections with the trajectories of the two attractors (blue and green) and that of basin boundary (red) are indicated. The parameter values are, $K = 1, k_1 = 0.5, k_2 = 0.5, r = 1, d_1 = 0.078, d_2 = 0.024, a_1 = 0.63, a_2 = 0.1, \epsilon_1 = 2.22$ and $\epsilon_2 = 1.18$.

Figure 5. LER and the result of numerical perturbation experiment for the three-species food chain model. (a) Population dynamics of smaller-amplitude cycles (black line: basal species, gray line: first consumer, dotted line: top predator), the corresponding LER (c) and the transition rate (e) in the numerical perturbation experiment (100 simulation trials, $\sigma_m = 0.05$). (b) Population dynamics of larger-amplitude cycles, the corresponding LER (d) and the transition rate (f).

Figure 6. Phase space plot of the two attractors and the result of basin boundary analysis for the two-predator one-prey model. (a) Two limit cycles in a three-dimensional phase space (blue: predator 1 and prey, green: predator 2 and prey). (b) Basin boundary between the two limit cycles approximated by 250 trajectories obtained from the straddle orbit method (shown in red). (c) Basins for limit cycle with predator 1 (light gray) and limit cycle with predator 2 (dark gray) in the 2D plane shown in (b). Intersections with the trajectories of the two attractors (blue and green) and that of basin boundary (red) are indicated. The parameter values are, $K = 1, k_1 = 0.5, k_2 =$

754 $0.5, r = 1, d_1 = 0.37, d_2 = 0.52, a_1 = 2.37, a_2 = 4, b_{12} = 0.90, b_{21} = 0.82$ and
 755 $\epsilon = 2$.

756

757 Figure 7. LER and the result of numerical perturbation experiment for the
 758 two-predator one-prey model. (a) Population dynamics of limit cycles with
 759 predator 1 and prey (black line: prey, gray line: predator 1, dotted line:
 760 predator 2), the corresponding LER (c), and the transition rate (e) in the
 761 numerical perturbation experiment (100 simulation trials, $\sigma_m = 0.05$). (b)
 762 Population dynamics of limit cycles with predator 2 and prey, the
 763 corresponding LER (d), and the transition rate (f).

764

765 Figure 8. Vulnerability index (VI) and the transition rate (100 simulation
 766 trials at each σ_m) in the numerical perturbation experiment for (a, b) the
 767 one-predator-two-prey model, (c, d) the three-species food web model, and (e,
 768 f) the two-predator-one-prey model. Black lines and points represent the
 769 three-species chaos, the large-amplitude limit cycle and the predator 1
 770 dominant limit cycle, respectively, and gray lines and points indicate the
 771 two-species limit cycle, the small-amplitude limit cycle and the predator 2
 772 dominant limit cycle, respectively. $T = 10000, 5000$, and 5000 for VIs in (a),
 773 (c) and (e), respectively. Lines in (b), (d) and (f) represent smoothed
 774 transition rates by taking 20-points moving average.

775

776 Figure B.1. Bifurcation diagram of the one-predator two-prey model drawn
 777 by the continuation method over the range of b_{12} with different a_1 values.
 778 The black points indicate maxima and minima of the population density of
 779 prey 2. The arrows indicate b_{12} values between which the system is bistable.
 780 Below the b_{12} value indicated by “TC”, the stable prey 2 equilibrium loses
 781 stability by a transcritical bifurcation where the equilibrium collides with an
 782 unstable two species equilibrium (with prey 1 and prey 2). In contrast, above
 783 the b_{12} value indicated by “C”, the chaotic attractor disappears because of a
 784 boundary crisis (the chaotic attractor comes into contact with the basin
 785 boundary). The parameter values are the same to those in Figure 2 except for
 786 a_1 and b_{12} .

787

788 Figure B.2. Bifurcation diagram of the three-species food chain model over
 789 the range of a_1 with different a_2 values drawn by the continuation method.

790 The black points indicate maxima and minima of the population density of
 791 the top predator. There are period doubling bifurcations in (d), (e) and (f).
 792 The arrows indicate a_1 values between which the system is bistable. There
 793 are saddle-node bifurcations of limit cycles on the both sides of the a_1 values
 794 (indicated by “SN1” and “SN2”) except for (f). The parameter values are the
 795 same to those in Figure 4 except for a_1 and a_2 .

796
 797 Figure B.3. Bifurcation diagram of the two-predator one-prey model drawn
 798 by the continuation method over the range of b_{12} with different a_1 values.
 799 The black points indicate the maxima and minima of the prey population
 800 density. The arrows indicate b_{12} values between which the system is
 801 bistable. Above the b_{12} value indicated by “TC1”, the limit cycle with
 802 predator 2 and the prey loses stability by a transcritical bifurcation where it
 803 collides with an unstable periodic orbit with three-species. In contrast, below
 804 the b_{12} value indicated by “TC2”, the limit cycle with predator 1 and the
 805 prey in turn loses stability by colliding with the unstable periodic orbit. The
 806 parameter values are the same to those in Figure 2 except for a_1 and b_{12} .

807

(a)

(b)

(c)

(a)

(b)

(c)

(d)

(e)

(f)

(a)

(b)

(c)

(a)

(b)

(c)

(a)

(b)

(c)

(d)

(e)

(f)

(a)

(b)

(c)

(d)

(e)

(f)

(a)

(b)

(c)

(d)

(e)

(f)