



Ecological resilience of population cycles: A dynamic perspective of regime shift



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HIGHLIGHTS

- We developed a numerical method that can provide the structure of the division of alternative cyclic dynamics.
- We applied our method to different three-species systems in order to understand the ecological resilience of the systems showing cyclic dynamics.
- Our results suggested that the temporal variation of ecological resilience in cyclic dynamics cannot be understood straightforwardly because of the complex structure of the basin boundaries.

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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.

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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

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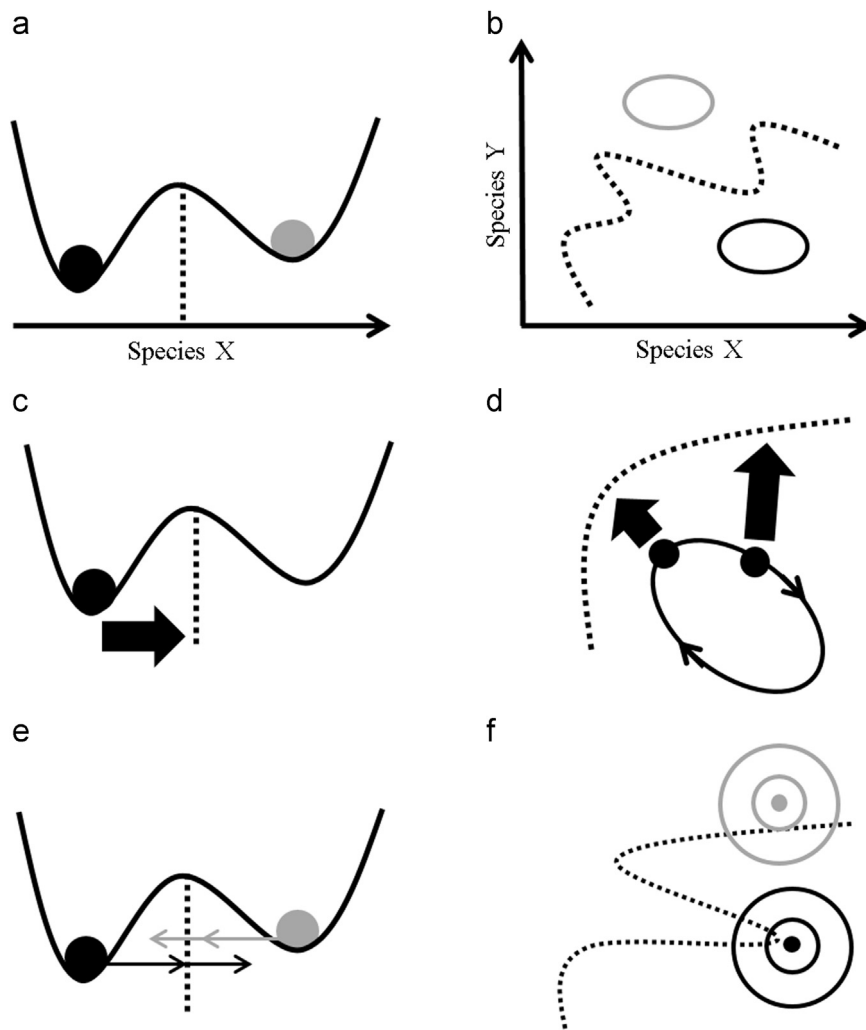


Fig. 1. The difference between stability of equilibrial states divided by an unstable equilibrium and that of oscillatory dynamics divided by a basin boundary. (a) A potential description explaining ecological resilience. Solid line describes the stability of equilibria. Dotted line indicates the position 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).

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

Theoretical studies have predicted ASS in ecological systems since the 1960s (Lewontin, 1969; Holling, 1973; May, 1977), and the existence of ASS has been suspected in a wide range of natural

systems [marine systems, Petraitis and Dudgeon (2004), Daskalov et al. (2007); lakes and ponds, Cottenie et al. (2001), Carpenter et al. (2011); rivers, Dent et al. (2002); terrestrial systems, McCune and Allen (1985), Ripple and Beschta (2006)]. However, empirical findings obtained from non-experimental approaches offer only indirect evidence of ASS and are still open for alternative explanations. In contrast, manipulation experiments provide direct evidence for the presence or absence of ASS. Schröder et al. (2005) reviewed 35 manipulative experiments and found that 13 of them showed clear evidence for ASS, whereas 8 demonstrated the absence of ASS (14 studies were not appropriate tests for ASS in their criteria). More importantly, stable states in the five experiments showing ASS included population fluctuations. Based on this finding, they insisted that “it is not surprising that ASS can also contrast in the type of their intrinsic dynamics” (e.g., Murdoch et al., 2002; De Roos and Persson, 2003; Wearing et al., 2004; McCauley et al., 1999; Henson et al., 2002; Zamamiri et al., 2001), although “ASS are still often perceived as contrasting equilibrium values where a system exhibits fix-point stability in each of its states” (e.g., Beisner et al., 2003).

In the present study, based on the “straddle orbit” (Battellino et al., 1988; Grebogi et al., 1988), a method to approximate the

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