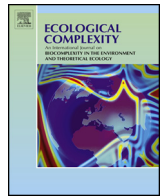




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Original Research Article

## Alternative (un)stable states in a stochastic predator–prey model

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### ABSTRACT

Stochastic models sometimes behave qualitatively differently from their deterministic analogues. We explore the implications of this in ecosystems that shift suddenly from one state to another. This phenomenon is usually studied through deterministic models with multiple stable equilibria under a single set of conditions, with stability defined through linear stability analysis. However, in stochastic systems, some unstable states can trap stochastic dynamics for long intervals, essentially masquerading as additional stable states. Using a predator–prey model, we demonstrate that this effect is sufficient to make a stochastic system with one stable state exhibit the same characteristics as an analogous system with alternative stable states. Although this result is surprising with respect to how stability is defined by standard analyses, we show that it is well-anticipated by an alternative approach based on the system's "quasi-potential." Broadly, understanding the risk of sudden state shifts will require a more holistic understanding of stability in stochastic systems.

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### 1. Introduction

When an ecological system has alternative stable states – multiple stable equilibria in its underlying deterministic dynamics – very interesting behaviors can result (May, 1977). For instance, switching between alternative stable states through time can occur either by a stochastic perturbation to the state itself that moves the system into the alternative basin of attraction, or by a perturbation to the external conditions that moves the system out of the multi-stable regime (Fig. 1a; Beisner et al., 2003; Ridolfi et al., 2007; Scheffer, 2009). It is alarming that small perturbations can produce large state changes, and that an equal size perturbation in the reverse direction will not return the system to the original state (Fig. 1a).

Traditionally in ecology, alternative stable states in models are identified through linear stability analysis, wherein the dynamics following a perturbation from an equilibrium state are characterized via linear approximation. Decay of perturbations means convergence to the equilibrium, and thus stability of that equilibrium state. These perturbations are assumed to be very small, so that the linear approximation is valid, and isolated, so

their growth or decay can be examined without considering further perturbations.

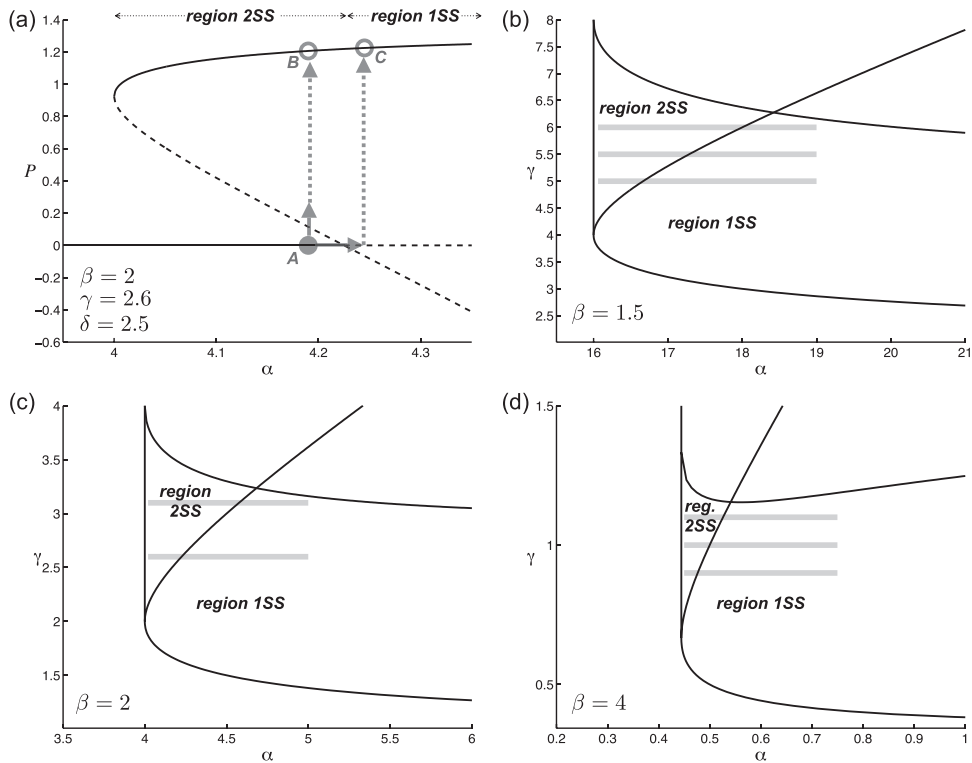
Ecological dynamics are driven by both deterministic and stochastic components (Ellner and Turchin, 1995; Bjørnstad and Grenfell, 2001; Coulson et al., 2004; Denaro et al., 2013), but linear stability analysis only examines a system's deterministic behavior following a single, small, isolated perturbation. In this way, this ubiquitous technique is ill-equipped to address situations where stochasticity has a meaningful, qualitative effect on dynamics (e.g. Chesson and Warner, 1981; Vilar and Solé, 1998; Anderies and Beisner, 2000; Hastings, 2001; Mankin et al., 2002; Greenman and Benton, 2003; Spagnolo et al., 2003, 2004; Valenti et al., 2004a; Abbott et al., 2009). Counter-intuitive qualitative effects arise from the interaction between stochasticity and nonlinearities. These effects include noise enhanced stability and stochastic resonance (Gammaitoni et al., 1998; Valenti et al., 2004b). The transient behaviors of stochastic systems are intriguingly complex, as they can approach a stable state in a multitude of ways (Fiasconaro et al., 2003; Fukami and Nakajima, 2011) or avoid convergence on a stable state altogether (Ridolfi et al., 2007). As a result of these complex behaviors, deterministic analyses can miss important features of stochastic systems (Spagnolo et al., 2003; Provata et al., 2008). In this paper, we explore the implications of this disconnect specifically for the study of alternative stable states.

Classic theory has focused on using linear stability analysis to identify stable equilibria, under the assumption that these are the

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**Fig. 1.** Bifurcation diagrams for deterministic model (1), with alternative stable states in the “region 2SS” range. (a) Equilibrium predator density versus  $\alpha$ . Solid lines represent stable equilibria and dashed lines are unstable or infeasible (i.e. negative) equilibria. A population at A can shift to the upper equilibrium by direct perturbation to its density (to arrive at B), or by a perturbation in  $\alpha$  (to arrive at C). Populations at B or C subjected to an equal but opposite perturbation will recover to B, not A. (b–d) Diagrams showing regions 1SS and 2SS in  $\alpha$ – $\gamma$  space for 3  $\beta$  values. Horizontal gray stripes show  $\gamma$  values and  $\alpha$  ranges used with each  $\beta$  in our simulations. (Note,  $\delta$  affects the equilibrium population sizes but not the locations of these regions, so these diagrams hold for any value of  $\delta$ . Noise intensity,  $\sigma$ , is by definition 0 in the deterministic model depicted here.)

only states that matter in the long-term. However, many fascinating and well-documented examples exist where there is a clear long-term influence of unstable equilibria (Rohani et al., 2002; Coulson et al., 2004; D’Odorico et al., 2005; Mankin et al., 2007; Tél, 1990; Rand and Wilson, 1991; Aparicio and Solari, 2001; Greenman and Benton, 2003; Dwyer et al., 2004). For example, saddle nodes, equilibria that are unstable yet attracting from some states along a stable manifold, can cause a stochastic trajectory to remain nearby for long, albeit transient, intervals (Cushing et al., 1998; Henson et al., 1999; Hastings, 2004; Parker et al., 2011). Continual stochastic perturbations can allow frequent visits to such a saddle. In this way, systems could appear as though they have alternative stable states even when classic theory says they do not. Currently, we lack theory on whether it is possible or even informative to distinguish between true (classical) multi-stability and stochastic look-alikes (Fukami and Nakajima, 2011), making applications of these concepts to data particularly challenging.

In this paper, we study a stochastic version of a predator–prey model (Freedman and Wolkowicz, 1986; Kot, 2001) that allows us to compare dynamics from highly analogous systems with and without alternative stable states in their underlying deterministic skeletons. We find that several key characteristics that we would normally associate with alternative stable states appear even when the model has only a single stable equilibrium. This occurs when a saddle effectively poses as an additional attractor, as described above. It may not be strictly impossible to distinguish between systems with true alternative stable states and other stochastic systems with similar dynamics, but our results demonstrate that the distinction is likely to be significantly more subtle than is generally recognized, and that the stable/unstable classification dichotomy should be reconsidered.

Because we find that sudden state shifts may occur even in the absence of “alternative stable states” (as defined through classical linear stability analysis), our results challenge us to seek more informative measures of stability for stochastic systems. We recently proposed the quasi-potential as a useful means of quantifying and visualizing stability in stochastic ecological models (Nolting and Abbott, 2016). We therefore close this article by exploring whether “stability” as measured by the quasi-potential better aligns with the stochastic behavior of the model.

## 2. Methods

### 2.1. Model

One step toward a better understanding of alternative stable states is to better appreciate whether and how they differ from other types of stochastic dynamics. We explore this issue beginning with a deterministic predator–prey model (Freedman and Wolkowicz, 1986),

$$\frac{dN}{dt} = N \left( 1 - \frac{N}{\gamma} \right) - \frac{NP}{(1/\alpha)N^2 + N + 1} \quad (1a)$$

$$\frac{dP}{dt} = \frac{\beta\delta NP}{(1/\alpha)N^2 + N + 1} - \delta P, \quad (1b)$$

where  $N$  and  $P$  are prey and predator population densities,  $\gamma$  is a rescaled prey carrying capacity,  $\beta$  governs the rate at which consumed prey are converted to predator population growth, and  $\delta$  is the predator’s rescaled death rate. We deliberately use the same parameterization here as Kot (2001, Chapter 9), to which we refer

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