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A stylized model of stochastic ecosystems with alternative stable states

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Abstract

We construct a generic ecosystem model that features the basic mechanisms of alternative stable states as well as two different stochastic influences. In particular, we use a mean-reverting jump-diffusion process to model the evolution of the ecosystem state over time. We review key concepts of multistability theory and the simple heuristics commonly employed to illustrate them. We then provide mathematical definitions for these concepts in the model context. Our contribution to the literature is twofold: we improve the representation of stochasticity in, and clarify key concepts of, multistability theory. The simplicity of the model enables a number of applications, such as finding economically optimal management strategies, identifying criteria for sustainable ecosystem management in a stochastic viability framework, deriving the probability of a regime shift, or empirically identifying the factors which have caused a specific regime shift.

Recommendations for resource managers:

- Stochasticity is an important feature of multistable ecosystems and may by itself cause abrupt regime shifts. This highlights the role of active resilience management.
- Previously deemed safe management strategies can trigger undesired regime shifts under changed

environmental conditions. Hence, managers need to adapt to changing conditions.
- Different types of management actions come with different probabilities of (un)desired regime shifts.

KEYWORDS
critical thresholds, ecosystem management, multistability, regime shift, resilience, stochastic process, tipping points

1 | INTRODUCTION

Many ecosystems are characterized by a duality of apparent stability and a surprising susceptibility to abrupt changes in the ecosystem's state and services (Petraitis, 2013). These changes, or: regime shifts, often occur in a catastrophic manner and may be difficult or impossible to reverse (Scheffer et al., 2001). Regime shifts have been observed, for example, in shallow lakes, coral reefs, grasslands, and fisheries (Folke et al., 2004) and have been hypothesized for global systems like the Amazon rainforest (Lovejoy & Nobre, 2018), the Antarctic Ice Sheet (Rosier et al., 2021), or the Earth's climate at large (Steffen et al., 2018).

The prevalent concept to explain this behavior is the notion of alternative stable states going back to the seminal works of Lewontin (1969), Holling (1973), Noy-Meir (1975), and May (1977). This means that more than one stable equilibrium state of the ecosystem exists for given environmental conditions. The related concepts of critical thresholds, tipping points, and resilience have been particularly influential and have stimulated research across disciplines as well as informed policy and management of ecosystems (Barnosky et al., 2012; Beisner et al., 2003; Dakos et al., 2019; Folke, 2006; Lenton et al., 2008; Ludwig et al., 1997; Scheffer, 2009; Walker et al., 2004). Beyond its sound conceptual core, the success of multistability theory has also been due to the appealing intuitiveness with which it has been propagated. In particular, the use of heuristic devices to reduce complex stochastic interactions and processes in ecosystems to a deterministic, mechanistic relationship makes the theory easy to communicate. The dichotomy between complex reality and simple theory has necessarily rendered many of the key concepts fuzzy and weakened conceptual boundaries. In part, the use of multistability theory as a "boundary object" (Brand & Jax, 2007) has been useful to facilitate the exchange of ideas across disciplinary borders (Strunz, 2012). However, imprecise terminology and lack of conceptual clarity have also led to confusion and have created a divide between researchers with different understandings of concepts like alternative stable states, thresholds, or resilience.

In this paper, we construct a generic ecosystem model that incorporates the key elements of multistability theory as well as two different stochastic influences: continuous diffusion and discrete jumps. While the model is more detailed and complex in its treatment of stochasticity, it is simple enough to provide rigorous definitions and a clear understanding of alternative stable states. It thus helps bringing together different discourses of ecosystems with alternative stable states. In addition, our model easily lends itself to a number of applications, such as finding economically optimal management strategies, identifying criteria for sustainable ecosystem management in a stochastic viability framework, deriving the probability of a regime shift, or empirically identifying the factors which have caused a specific regime shift.

In particular, we use a mean-reverting jump-diffusion process to model the evolution of the ecosystem state over time. Jump-diffusion processes have been used in fields as diverse as finance (Merton, 1976), soil hydrology (Daly & Porporato, 2006), or neuroscience (Jahn et al., 2011), but not yet to capture stochasticity in ecosystems with alternative stable states. In this context, either pure diffusion or pure jump processes have been used. Continuous diffusion has been used to capture natural fluctuations in ecosystems, for example, in models of lake eutrophication (Contamin & Ellison, 2009) or early warning signals for regime shifts (Biggs et al., 2009). Mäler et al. (2007) used a specific diffusion process—an Ornstein-Uhlenbeck process—to model natural groundwater table dynamics. Jump processes have been used to model rare disturbances such as fire in savannahs that may switch between tree-dominated and grassland-dominated states (D'Odorico et al., 2006). Our model combines and enhances these existing approaches: we extend the basic Ornstein-Uhlenbeck model by introducing a novel bistability mechanism for endogenous reversible regime shifts and adding a jump process to allow for infrequent disturbances of the ecosystem state.

The paper is organized as follows. In the next section, we review the key concepts and mechanisms of the theory of alternative stable states in ecology. In Section 3, we formalize these concepts in a mathematical ecosystem model and introduce stochastic dynamics. In Section 4, we sketch a number of potential applications of the model. In Section 5, we discuss our model and conclude.

2 | THEORETICAL FRAMEWORK

The prevalent concept to explain how abrupt changes in state variables may arise in response to gradual changes in environmental conditions is the notion of alternative (or: multiple) stable states (e.g., Beisner et al., 2003; May, 1977; Petraitis, 2013; Scheffer et al., 2001). This means that more than one stable equilibrium of the state variables exists for given environmental conditions. Alternative equilibria are stabilized by negative feedbacks that counteract deviations of state variables from stable equilibria (DeAngelis et al., 1986) due to perturbations. The domains in state space in which negative feedbacks cause the state variables to return to the same equilibrium after a perturbation are called *basins of attraction*. The boundary between two basins of attraction is called the *separatrix* or "breakpoint curve" (May, 1977) and contains an unstable equilibrium point of the ecosystem state (Petraitis, 2013). An intuitive way to visualize this is the ball-and-cup heuristic, also called stability landscape. Figure 1 shows such a diagram for the simplest possible case with one state variable and two locally stable equilibria.

The horizontal axis measures the value of the state variable, the vertical axis shows the dynamic potential of the system. The position of the ball in the landscape represents the stability of the ecosystem: the ball always rolls downhill; the force attracting the ball are ecological feedbacks. The shape of the landscape is determined by, and constant for, given environmental conditions. Points where the ball comes to rest are equilibria, valleys are basins of attraction. If the ball is pushed over the ridge by a sufficiently strong perturbation the state variable moves into the other basin of attraction ("basin crossing") where feedbacks induce a convergence to the alternative equilibrium. As a consequence, a potentially large shift in the ecosystem state occurs, where the extent of the shift depends on environmental conditions.

Figure 2 illustrates the effect of changing environmental conditions on the equilibrium ecosystem state. For a low level of conditions only one equilibrium exists at a relatively large

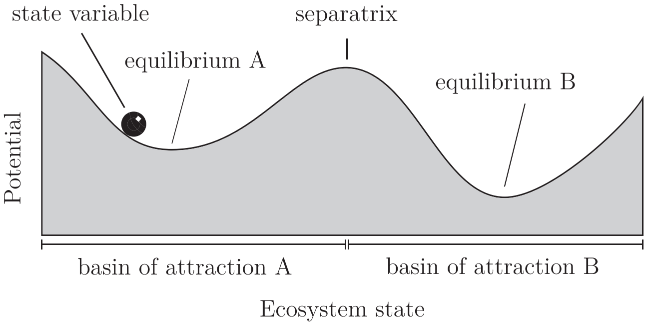

FIGURE 1 Ball-and-cup diagram.

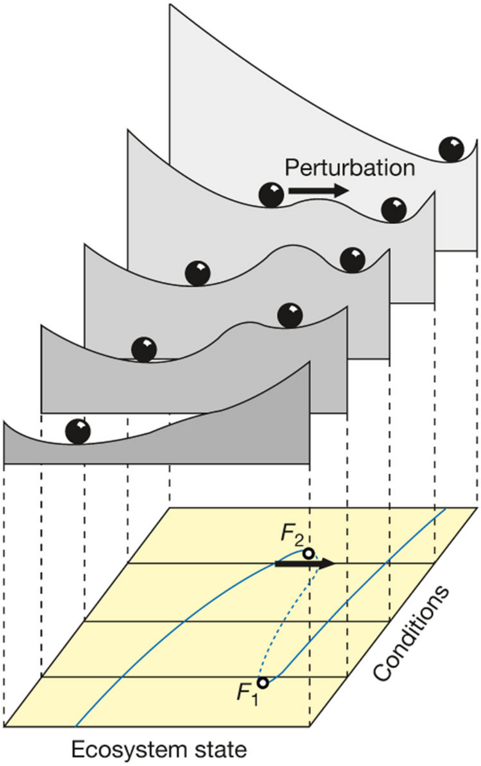

FIGURE 2 Ball-in-cup diagram and ecosystem response curve: two heuristic devices to illustrate alternative stable states. Reprinted from Scheffer et al. (2001) with permission from Springer Nature.

value of the state variable. As illustrated in the corresponding stability landscape above, this equilibrium is globally stable, since the ball will always return to the same single valley floor. As conditions increase the stability landscape changes and a second locally stable equilibrium emerges. This enables the possibility of crossing the boundary between alternative basins of attraction due to a perturbation. In this more detailed illustration a second mechanism for abrupt shifts becomes apparent: when conditions change further beyond a level corresponding to point F_2, the first stable equilibrium ceases to exist. If the state variable was attracted by this equilibrium before the feedbacks to the state variable change suddenly, causing an abrupt shift in the ecosystem state ("critical transition").

Reversing environmental conditions to preshift levels after a critical transition does not necessarily entail a return of the state variable to preshift levels. Ensuring a reverse shift would require changing environmental conditions below a level corresponding to point F_1. The phenomenon that forward and reverse shifts occur at different critical conditions is known as *hysteresis* and makes critical transitions very difficult to reverse (Scheffer et al., 2001).

Ecosystems exhibit alternative stable equilibria only over a certain range of environmental conditions known as the *bifurcation set*—the range of conditions between the *bifurcation points* F_1 and F_2 in Figure 2. These points mark the location of a fold (or: saddle-node) bifurcation where a single equilibrium bifurcates (or: splits) into three—two locally stable and one unstable—and nonlinear dynamics become possible (Petraitis, 2013). The bifurcation points[1] correspond to critical levels of environmental conditions at which critical transitions between alternative stable states occur. Figure 3 shows the ecosystem response curve in more detail by rotating the bottom plane of Figure 2 clockwise by 90°.

The red arrows represent the effect of ecological feedbacks on the state variable. For constant environmental conditions (i.e., a fixed position on the horizontal axis) the arrows indicate in which direction on the vertical axis the state variable is attracted. The blue curve contains all equilibria of the state variable across a range of conditions. The solid upper and lower branches contain stable equilibria, the dotted section in between represents unstable equilibria on the boundary between the basins of attraction (separatrix). We should distinguish between individual equilibrium points with distinct values of the state variable and collections of equilibrium points with similar, but different values of the state variable. The terms alternative stable states, dynamic regimes, and equilibria are often used interchangeably for one or the other concept. We use the terms as follows: for given environmental conditions an *equilibrium* is a unique point on the blue curve with zero rate of change of the state variable and a distinct numerical value attached to it. In contrast, a *dynamic regime* is a set of many equilibrium points and the feedbacks stabilizing them across different environmental conditions—meaning a whole branch of the blue curve and the basins of attraction surrounding it (Scheffer & Carpenter, 2003). Dynamic regimes typically

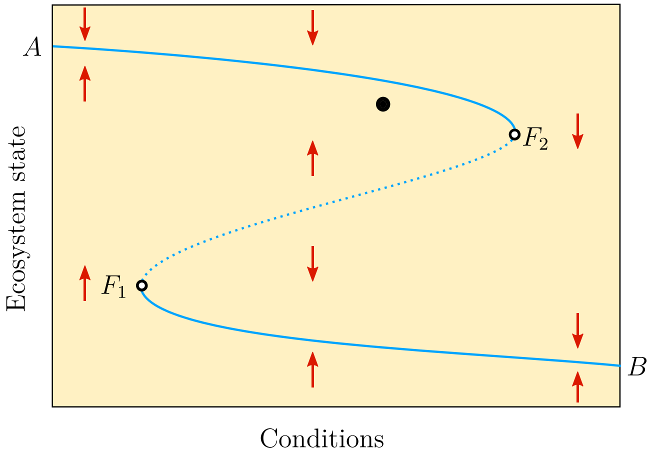

FIGURE 3 Ecosystem response curve. Redrawn from Scheffer et al. (2001) with permission from Springer Nature.

consist of qualitatively similar equilibrium states of the ecosystem with relatively small variation in the equilibrium value of the state variable across a wide range of conditions. For instance, a shallow lake may be in a clear, oligotrophic or a turbid, eutrophic regime.[2] With this, a *regime shift* is defined as a shift from one dynamic regime to the alternative one.

In Figure 3, the vertical distance between the current value of the state variable (indicated by a black dot) and its threshold value (represented by the dotted line) may be interpreted as a measure of resilience (Kinzig et al., 2006).[3] In an elementary sense we understand resilience as a descriptive ecological concept meaning the amount of disturbance an ecosystem can absorb without changing its basic function, structure, identity, and controls (Gunderson & Holling, 2001; Walker et al., 2004). In the particular case of a single state variable we define *resilience* as the maximum possible magnitude of a perturbation of the state variable without entering an alternative basin of attraction. Resilience changes considerably with varying environmental conditions (Carpenter, 2003).[4]

So far, we have discussed the theory of alternative stable states in a deterministic world in which the dynamic behavior of ecosystems is predictable. In reality, ecosystems are subject to stochastic perturbations arising from continuously occurring fluctuations and rare disturbances which cause unexpected and random behavior. In this uncertain world resilience is a key property of ecosystems with alternative stable states, because it determines the likelihood of flipping from one regime to the other (Gunderson & Holling, 2001). In many cases, erosion of resilience by changing environmental conditions makes the shift to an alternative regime due to stochastic perturbations more likely (Scheffer & Carpenter, 2003). We focus on the interaction between stochastic perturbations and the two key deterministic mechanisms for regime shifts (basin crossing and critical transitions) in detail in the next section and leave aside other mechanisms for the occurrence of abrupt shifts in state variables, such as phase shifts (Scheffer et al., 2001).

3 | MODEL

We now develop a formal model based on the concepts discussed in the previous section. We first present the deterministic dynamics under constant conditions, before turning to stochasticity and changing environmental conditions. Finally, we introduce management.

3.1 | Deterministic dynamics, states, and regimes of the system

At any point in time $t \in [0, \infty)$, the state of the ecosystem is characterized by the value of a continuous state variable $X_t \geq 0$, which captures the numerical value of some important quantity in the system, for instance the spawning stock biomass of a fish species or an index of the (multidimensional) ecosystem state. Its evolution over time is given by:

$$\frac{dX_t}{dt} = \theta(\mu(c) - X_t) + \frac{dZ_t}{dt}, \tag{1}$$

where $\theta > 0$ parametrizes the strength of feedbacks from ecological processes to the state variable. The parameter $\mu(c)$ determines the equilibrium value of X_t in the absence of stochastic influences and depends on the underlying environmental conditions, which are denoted by the normalized parameter $c \in [0, 1]$. For now, c is constant; we consider changing environmental conditions in Section 3.3. Z_t represents stochastic perturbations, such as fluctuations in external forcing or rare events like pest outbreaks. To start with, we discuss the deterministic part of (1) (i.e., the first summand) and elaborate on the stochastic component in Section 3.2. That is, we set $Z_t = 0$ for all t. Then, the evolution of the state variable is given by:

$$X_t = X_0 \mathrm{e}^{-\theta t} + \mu(c)(1 - \mathrm{e}^{-\theta t}). \tag{2}$$

The *deterministic equilibrium* satisfies $dX_t/dt = 0$ with $Z_t = 0$ and, from Equation (1), is given by $X_t = \mu(c)$. Thus, the equilibrium ecosystem state is determined by environmental conditions, as proposed by multistability theory (Figure 3). The rate of increase of the state variable is positive when $X_t < \mu(c)$ and negative when $X_t > \mu(c)$. Thus, deterministic equilibria of (1) are stable. The rate at which the state variable converges to its deterministic equilibrium $\mu(c)$ is determined by the parameter θ. The larger θ, the greater the speed of convergence toward the equilibrium value. Equation (1) describes an ecosystem with multiple stable states when $\mu(c)$ takes on more than one possible value for a given level of c across a certain range of environmental conditions. In particular, the bi-stable case depicted in Figure 3 is obtained when there are three possible values of $\mu(c)$ for a given value of c across the range of conditions $F_1 \leq c \leq F_2$ (corresponding to the interval on the horizontal axis between the bifurcations points in Figure 3). In this case, one may rewrite (1) as:

$$\frac{dX_t}{dt} = \begin{cases} \theta(\mu_A(c) - X_t) + \dfrac{dZ_t}{dt}, & \text{for } 0 \leq c < F_1, \\ & \text{or } F_1 \leq c \leq F_2 \ \wedge \ X_t > \mu_*(c), \\ \dfrac{\mathrm{d}Z_t}{\mathrm{d}t}, & \text{for } F_1 \leq c \leq F_2 \ \wedge \ X_t = \mu_*(c), \\ \theta(\mu_B(c) - X_t) + \dfrac{dZ_t}{dt}, & \text{for } F_1 \leq c \leq F_2 \ \wedge \ X_t < \mu_*(c), \\ & \text{or } F_2 < c \leq 1, \end{cases} \tag{3}$$

where $\mu_*(c)$ represents unstable equilibria located on the separatrix (corresponding to the dotted blue line in Figure 3) with a corresponding *threshold value* of the state variable that varies with environmental conditions. If $X_t > \mu_*(c)$ the deterministic equilibrium is given by $\mu_A(c)$, and by $\mu_B(c)$ if $X_t < \mu_*(c)$. Together with (1), it follows that $\mu_A(c)$ and $\mu_B(c)$ are locally stable equilibria of X_t. In Figure 3, equilibria with subscript A are points located on the upper branch of the blue curve in Figure 3, those with subscript B on the lower branch. The basins of attraction $b[\mu_A(c)]$ and $b[\mu_B(c)]$ comprise the set of all points in state space that converge over time either to $\mu_A(c)$ or to $\mu_B(c)$, respectively, for given environmental conditions:

Definition 1. The *basin of attraction* $b[\mu(c)]$ is the set of all values of X_t for which

$$\lim_{t \to \infty} X_t = \mu(c), \tag{4}$$

given Equations (1), (3) and $Z_t = 0$ for all t.

To generalize these concepts to different environmental conditions we additionally define the concept of *dynamic regimes*—collections of qualitatively similar equilibrium states of the ecosystem across a range of environmental conditions, such as a clear and a turbid regime across different nutrient levels in a shallow lake. This corresponds to the solid upper and lower branches of the blue curve in Figure 3. The dynamic regimes r_A and r_B encompass the set of all basins of attraction corresponding to equilibria with subscript A or B, respectively, over the entire range of conditions:

$$r_A = \{b[\mu_A(c)]\}_{c=0}^{F_2}, \; r_B = \{b[\mu_B(c)]\}_{c=F_1}^{1}. \tag{5}$$

With that, a *regime shift* occurs when the state variable moves from one regime into the alternative regime. We assume that the ecosystem is initially in regime r_A. At the time of a regime shift the feedbacks to the state variable change abruptly, but not necessarily the value of the state variable itself. Only over time does X_t converge to the alternative equilibrium $\mu_B(c)$, where θ determines the speed of convergence.

3.2 | Stochastic dynamics

We now specify the stochastic component Z_t to incorporate continuous diffusion and discrete jumps, and analyse its consequences for the system dynamics. To focus on the stochastic dynamics, we begin with a case in which only one stable equilibrium exists (i.e., $c < F_1$ or $c > F_2$) and regime shifts are not possible. Multiplying (1) by dt and specifying $dZ_t = \sigma dW_t + ydN_t$, the evolution of the state variable over time is given by the stochastic differential equation

$$dX_t = \theta(\mu(c) - X_t)dt + \sigma dW_t + ydN_t. \tag{6}$$

The right-hand side consists of three additive components: a drift term $\theta(\mu(c) - X_t)$, a diffusion term σdW_t, and a jump term ydN_t. Hence, Equation (6) describes an Ornstein–Uhlenbeck (O–U) process[5] (the first two terms) with an additional jump process (the third term). The deterministic drift term, discussed in detail in Section 3.1, specifies the change in the expected value of the process over time—the *drift* of the stochastic process X_t (Schuss, 2010).

The diffusion term σdW_t captures continuously occurring perturbations to the state variable, for instance random events of individual mortality and reproduction in population dynamics (Lande et al., 2003). It consists of the diffusion coefficient σ which determines the relative influence of these perturbations on X_t, and the infinitesimal increment dW_t of a Wiener process. The Wiener process W_t describes Brownian motion: it is a series of identically and independently distributed (i.i.d.) random variables following a normal distribution with zero mean and time-dependent variance. That is, for all $0 \leq s < t$, one has $W_t - W_s \sim \mathcal{N}(0, t - s)$. The infinitesimal increment $dW_t = W_{t+dt} - W_t$ is thus a random variable with mean zero and variance dt.

The jump term ydN_t captures discrete jumps in the value of the state variable, which may arise from rare events like pest outbreaks or extreme weather events and occur at random times. Such behavior can be modeled by a compound Poisson process (Privault, 2013):

$$J_t = \sum_{j=1}^{N_t} y_j. \tag{7}$$

The size of jumps is modeled by a random variable y with i.i.d. realizations y_j drawn from a normal distribution with mean $\bar{y}$ and variance β^2. The individual jumps can be observed when they happen, for instance when a hurricane hits a reef and reduces the coral cover. The arrival of jumps follows a homogeneous Poisson counting process N_t with intensity $\lambda > 0$. That is, the probability of n jumps occurring up to time t is given by:

$$P(N_t = n) = \mathrm{e}^{-\lambda t}\frac{(\lambda t)^n}{n!}. \tag{8}$$

Over an infinitesimally small time interval dt, there may be either a single jump or no jump. Hence, the infinitesimal Poisson increment $dN_t = N_{t+dt} - N_t$ is drawn from a Poisson distribution with mean λdt (Chiarella et al., 2015):

$$dN_t = \begin{cases} 1 & \text{with prob.} \quad \lambda dt, \\ 0 & \text{with prob.} \quad 1 - \lambda dt. \end{cases} \tag{9}$$

Thus, a jump occurs with probability λdt in the time interval dt, causing the value of X_t to jump discontinuously by the random amount y_j at the jump time t_j. In between jumps, the state variable follows the O–U process. Table 1 summarizes the parameters of the overall process (6).

The stochastic differential Equation (6) describes the evolution of X_t over the infinitesimally small time interval dt. To obtain the evolution of X_t over the entire time interval $[0, \infty)$, we solve (6) with the initial condition $X_{t=0} = X_0 > \mu_*(c)$, given dW_t as the infinitesimal increment of a Wiener process and dN_t according to (7), (8), and (9). Assuming for the moment that no regime shifts occur (for instance, $c < F_1$ or $c > F_2$), this initial value problem has the general solution (Appendix A.1):

$$X_t = X_0\mathrm{e}^{-\theta t} + \mu(c)(1 - \mathrm{e}^{-\theta t}) + \sigma\int_0^t \mathrm{e}^{-\theta(t-s)}dW_s + \int_0^t \mathrm{e}^{-\theta(t-s)}y_s dN_s. \tag{10}$$

At time $t = 0, X_t$ is equal to the observable initial value X_0. For any later point in time, the deterministic part of (10) can be calculated. For the stochastic part, the realizations of the Wiener and compound Poisson process are not known ex ante, but one can calculate their expected value. The Wiener process has an expected value of zero by definition as its

TABLE 1 Parameters describing the stochastic process X_t.

	Symbol	Parameter name	Ecological interpretation
Drift term	θ	Mean reversion speed	Strength of ecological feedbacks
	$\mu(c)$	Mean reversion level (of diffusion process)	Deterministic equilibrium value (depending on conditions)
Diffusion term	σ	Diffusion coefficient	Strength of random fluctuations
Jump term	y	Jump size (random variable)	Magnitude of rare events
	$\bar{y}$	Mean jump size	Average magnitude of rare events
	β^2	Variance of jump size	Variability of rare events
	λ	Intensity of Poisson process	Frequency of rare events

increments are drawn from a normal distribution with zero mean. For the jump term, the expected value with respect to the frequency and size of jumps is given by:

$$\mathbb{E}_{y,dN}\left[\int_0^t \mathrm{e}^{-\theta(t-s)} y_s \, dN_s\right] = \bar{y}\,\frac{\lambda}{\theta}(1 - \mathrm{e}^{-\theta t}). \tag{11}$$

The expected value of the jump component of (10) consists of the expected size $\bar{y}$ and the arrival rate λ of jumps. The absolute value of this expression is decreasing in θ (proof in Appendix A.2), which means that the relative contribution of jumps to the expected value of the state variable depends negatively on the strength of deterministic feedbacks. The expected value of X_t is thus given by:

$$\mathbb{E}[X_t] = X_0 \mathrm{e}^{-\theta t} + \mu(c)(1 - \mathrm{e}^{-\theta t}) + \bar{y}\,\frac{\lambda}{\theta}(1 - \mathrm{e}^{-\theta t}), \tag{12}$$

and its variance is given by (Das, 2002):

$$\mathrm{Var}[X_t] = \frac{\sigma^2 + \lambda\beta^2}{2\theta}(1 - \mathrm{e}^{-2\theta t}) + \mathbb{E}[X_t]^2. \tag{13}$$

Over time, the expected value of X_t tends away from its initial value X_0 and toward $\mu(c)$ as a result of deterministic ecological feedbacks, but is perturbed by random jumps. In the limit, X_t converges to its stationary mean, which is known as *mean reversion*:

$$\lim_{t\to\infty} \mathbb{E}[X_t] = \mu(c) + \bar{y}\,\frac{\lambda}{\theta}. \tag{14}$$

That is, the state variable is expected to converge to its deterministic equilibrium $\mu(c)$ plus a deviation due to jumps. The expected deviation from the equilibrium due to rare events depends positively on the arrival rate λ and the mean size of jumps $\bar{y}$, and negatively on the strength of deterministic feedbacks θ, which counteract the effect of random jumps. These results only hold when a single value of $\mu(c)$ exists for a given level of c (i.e., $c < F_1$ or $c > F_2$) and regime shifts are not possible. When $\mu(c)$ may take on three values (i.e., $F_1 \leq c \leq F_2$), stochastic perturbations can induce endogenous regime shifts and we cannot make closed-form statements about the behavior of X_t over an infinite time horizon.

Consider the case of a single regime shift at time t_{RS} due to basin crossing under constant environmental conditions. At this point in time X_t falls below its threshold value $\mu_*(c)$ and the state variable moves from regime r_A into the alternative regime r_B. Once in the alternative regime, the feedbacks acting on the state variable change instantaneously and X_t is attracted by its alternative deterministic equilibrium $\mu_B(c)$. The evolution of X_t after the shift is described by the same stochastic process (10) as before, but resets at time t_{RS} with initial value $X_{t_{\mathrm{RS}}}$ and the alternative equilibrium $\mu_B(c)$. This is possible because the process X_t (Equation 6) fulfills the *Markov property*: future values of X_t depend solely on the current value of the process and not on past realizations—the process is memoryless. In case of a single regime shift at time t_{RS}, one can rewrite (10) more precisely as:

$$X_t = \begin{cases} X_0 \mathrm{e}^{-\theta t} + \mu_A(c)(1 - \mathrm{e}^{-\theta t}) + \sigma \int_0^t \mathrm{e}^{-\theta(t-s)} dW_s + \sum_{j=1}^{N_t} \mathrm{e}^{-\theta(t-t_j)} y_j & \text{for } 0 \le t < t_{\mathrm{RS}} \\ X_{t_{\mathrm{RS}}} \mathrm{e}^{-\theta(t-t_{\mathrm{RS}})} + \mu_B(c)(1 - \mathrm{e}^{-\theta(t-t_{\mathrm{RS}})}) + \sigma \int_{t_{\mathrm{RS}}}^t \mathrm{e}^{-\theta(t-s)} dW_s + \int_{t_{\mathrm{RS}}}^t \mathrm{e}^{-\theta(t-s)} y_s dN_s, & \text{for } t \ge t_{\mathrm{RS}} \end{cases} \tag{15}$$

where N_t is the number of jumps that have occurred up to time t and t_j is the time of jump j. At time t_{RS}, one has observed the times and sizes of all jumps up to this point and the first line of Equation (15) gives the value of X_t at every prior time from an ex post perspective. The further development beyond t_{RS} is not known ex ante: one can calculate the expected value based on the updated initial value of the state variable $X_{t_{\mathrm{RS}}}$, which is known with certainty. Equation (15) holds until the next regime shift happens, say at $t_{\mathrm{RS}2}$, when the process resets again. This succession of regime-shift-and-resetting can go on indefinitely, but updating (15) every time a regime shift occurs accurately describes the dynamics.

Figure 4 depicts the case of a regime shift due to basin crossing caused by a negative jump. In this realization of the stochastic process (15), the state variable is initially below its deterministic equilibrium $\mu_A(c)$ by which it is attracted continuously over time. Stochastic diffusion causes the state variable to fluctuate and thereby keeping it from actually reaching the equilibrium. The first jump at t_1 brings the state variable precariously close to its threshold value, but the system is able to recover from this perturbation due to ecological feedbacks. The second jump at t_2 is smaller, but stochastic diffusion counteracts the deterministic feedbacks. The next jump happens before the system can recover and pushes the state variable below its threshold value, causing a shift to the alternative regime r_B at time t_{RS}, That is, the ecosystem is resilient against the first two jumps, but cannot cope with the additional perturbation of another negative jump in its state of decreased resilience. When the stochastic process resets at time t_{RS} the expected value of the further development is formed anew. Over time, the new regime stabilizes itself as the state variable is attracted by its new deterministic equilibrium $\mu_B(c)$; resilience against a reverse shift back to the initial regime r_A increases.

Figure 5 shows a situation in which the state variable does not remain in regime r_B after crossing the threshold. After the shift the state variable fluctuates around its deterministic equilibrium $\mu_B(c)$ which is located close to the threshold. This represents a case where conditions are unfavorable for regime r_B (i.e., c is only slightly greater than F_1, compare Figure 3) and resilience against a shift to regime r_A is low. Stochastic diffusion causes the state variable to cross the threshold between the basins of attraction a second time at t_{REV}. After this reverse regime shift, the state variable quickly converges to its deterministic equilibrium $\mu_A(c)$ due to ecological feedbacks.

3.3 | Changing environmental conditions

So far, we have focused on ecosystem dynamics under constant environmental conditions. In reality, "conditions are never constant" (Scheffer et al., 2001). That is, we have

$$c = c(t) \text{ with } c(0) = c_0, \tag{16}$$

which influences the dynamics of the state variable by changing the deterministic equilibrium $\mu(c)$ as well as the threshold value $\mu_*(c)$ continuously over time.

FIGURE 4 Sample path for a random realization of the stochastic process X_t. Parameter values: $X_0 = 60, \mu_A(c) = 75, \mu_B(c) = 20, \mu_*(c) = 48, \theta = 1, \sigma = 5, \lambda = 0.4, \bar{y} = -10, \beta = 5$. The simulation was performed with the Euler–Maruyama discretisation scheme using time steps of $\Delta t = 0.05$.

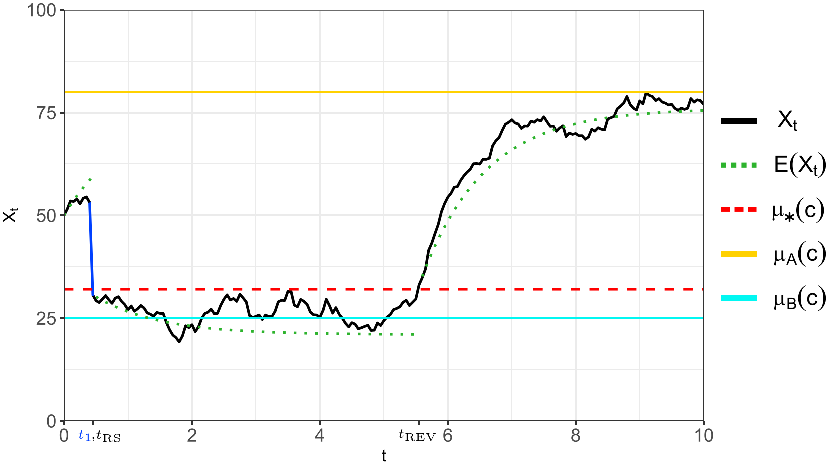

FIGURE 5 Sample path for a random realization of the stochastic process X_t. Parameter values: $X_0 = 50, \mu_*(c) = 32, \mu_A(c) = 80, \mu_B(c) = 25, \theta = 1, \sigma = 5, \lambda = 0.4, \bar{y} = -10, \beta = 10$. Again, $\Delta t = 0.05$.

For simplicity, we assume that changes in environmental conditions are deterministic and thus foreseeable.

Essentially, conditions are quantities in the ecosystem that change very slowly relative to state variables (Beisner et al., 2003).[6] A useful special case of (16), which we will assume in the following, is the basic exponential convergence process:

$$c_t = c_0 + \Delta c(1 - e^{-\gamma t}), \tag{17}$$

where Δc indicates the absolute change in normalized conditions c and γ parametrizes the rate of convergence. We assume that $0 < \gamma \ll \theta$, that is, environmental conditions change much less quickly than the state variable. When environmental conditions change, this modifies the equilibria of the system and the values of $\mu_A(c), \mu_B(c)$, and $\mu_*(c)$ change. That is, changing environmental conditions have no instantaneous effect on the value of state variable, but influence its deterministic trend over time and its susceptibility to regime shifts. Taken together, changing environmental conditions (Equation 17) and state dynamics (Equation 10) result in a continuously ongoing dual adjustment process.[7] Figure 6 illustrates the resulting dynamics.

As described in Section 2, changing environmental conditions pose an additional mechanism for regime shifts. If environmental conditions move beyond one of the bifurcation points, a critical transition to the alternative regime is inevitable, regardless of the value of the state variable. The mechanism for critical transitions is simple: when c increases beyond F_2, equilibrium $\mu_A(c)$ ceases to exist according to (3) and the state variable is attracted by the alternative equilibrium $\mu_B(c)$. Already before environmental conditions actually increase beyond F_2, a regime shift is likely to happen due to stochastic perturbations as a result of decreased resilience. The two mechanisms for regime shifts often act in combination. In general, a change in environmental conditions influences the resilience of the ecosystem to stochastic perturbations, which determines the likelihood of a regime shift (Gunderson & Holling, 2001, p. 50).

Once the state variable is in regime r_B, conditions need to be reversed to less than F_1 to ensure a reverse shift to regime r_A. Hence, our model captures hysteresis of the ecosystem state in response to changing environmental conditions.

3.4 | Ecosystem management

We include ecosystem management in the model as follows. There is a single ecosystem manager who chooses the type and intensity of a management action $a = \{v, q, z\}$ taken at time

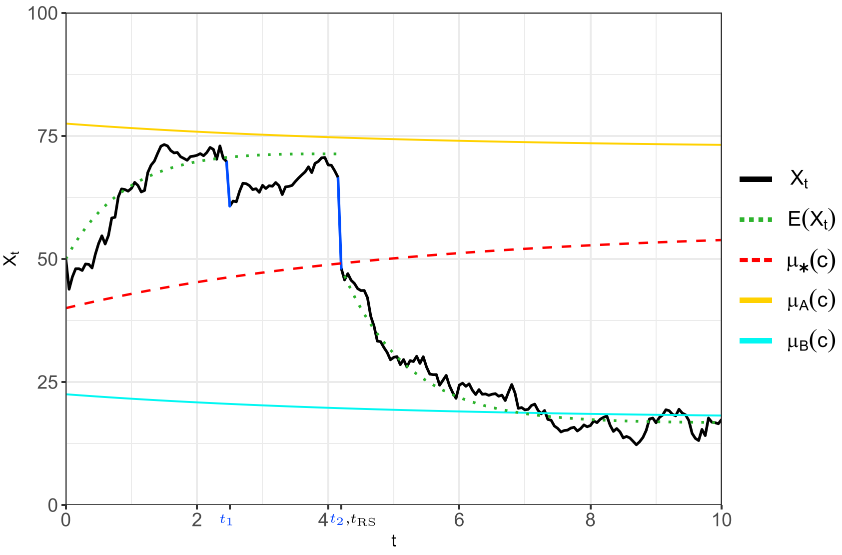

FIGURE 6 Sample path for a random realization of the stochastic process X_t. Parameter values: $X_0 = 50, \mu_A(c_t) = 90 - 25c_t, \mu_B(c_t) = 35 - 25c_t, \mu_*(c_t) = 80c_t, \theta = 1, \sigma = 5, \lambda = 0.3, \bar{y} = -10, \beta = 5,$ $c_0 = 0.5, \Delta c = 0.2, \gamma = 0.2$. Again, $\Delta t = 0.05$.

$t = 0$. There are three different types of management actions, each of which affects the ecosystem in a different way: type v directly and instantaneously influences the state variable, type q changes the environmental conditions over time, and type z modifies the system's susceptibility to stochastic influences.

Action $v > -X_0$ instantaneously changes the value of the state variable by the amount v at the time of action $t = 0$. Management may increase or decrease the value of the state variable. For instance, if the state variable is the biomass of a fish stock, harvesting a certain amount of fish immediately reduces the state variable by this amount while restocking increases it immediately. Other aspects of the stock dynamics, such as the equilibrium level of the state variable $\mu(c)$ or the threshold level $\mu_*(c)$ are unaffected by this type of management action. If no regime shift occurs the state variable tends to return to its equilibrium level over time due to ecological feedbacks. In this case, the time path of X_t resulting from taking management action v at time $t = 0$ is given by:

$$X_t(v) = (X_0 + v)\mathrm{e}^{-\theta t} + \mu_A(c_t)(1 - \mathrm{e}^{-\theta t}) + \sigma\int_0^t \mathrm{e}^{-\theta(t-s)}dW_s + \int_0^t \mathrm{e}^{-\theta(t-s)}y_s\,dN_s. \tag{18}$$

A shift to regime r_B may occur at any time in analogy to (15) and can be made either more or less likely by management action v. Indeed, for sufficiently strong actions, that is, $X_0 + v < \mu_*$, the state variable falls below its threshold value directly at the time of action $t = 0$ and a regime shift occurs with certainty.

Action $q \in [-c_0 - \Delta c, 1 - c_0 - \Delta c]$ changes the conditions over time by adding the amount q to the exogenous change in conditions Δc according to (17). Again, management may increase or decrease the conditions such that c_t lies in the normalized range [0, 1]. This type of management thereby modifies the deterministic equilibrium value $\mu(c)$ and the threshold value $\mu_*(c)$. In contrast to action v, action q does not change the value of the state variable directly, but influences its dynamics by changing the feedbacks acting on the state variable. Since conditions change only slowly relative to the state variable, actions of type q take a longer time to have the same quantitative effect on the state variable than actions of type v. In the example of fish in a lake, suppose there is anthropogenic nutrient loading of the lake, leading to an increase in resource availability for planktivorous fish. The higher availability of feed increases the spawning rates, which increases the equilibrium biomass $\mu(c)$ of planktivorous fish (assuming that death rates remain constant). Due to the Allee effect, increased resource availability may also result in a lower extinction threshold μ_* for the fish stock (Petraitis, 2013, Ch. 2.2). As conditions change over time to their new level $c_0 + \Delta c + q$ with rate γ, the state variable X_t adjusts incrementally to the modified equilibrium value $\mu_A(c_t)$ with rate θ (if no regime shift occurs):

$$X_t(q) = X_0\mathrm{e}^{-\theta t} + \mu_A(c_t(q))(1 - \mathrm{e}^{-\theta t}) + \sigma\int_0^t \mathrm{e}^{-\theta(t-s)}dW_s + \int_0^t \mathrm{e}^{-\theta(t-s)}y_s\,dN_s. \tag{19}$$

Action z modifies one or more of the stochastic parameters $\sigma, \bar{y}, \beta, \lambda$ by the amount z and is bounded by nonnegativity constraints for σ, β, and λ. With this action, management can modify the susceptibility of the state variable to stochastic perturbations. Examples would be dikes against floods or irrigation systems and water pumps against droughts. The modified time path of X_t is given by:

$$X_t(z) = X_0\mathrm{e}^{-\theta t} + \mu_A(c_t)(1 - \mathrm{e}^{-\theta t}) + \sigma(z)\int_0^t \mathrm{e}^{-\theta(t-s)}dW_s + \int_0^t \mathrm{e}^{-\theta(t-s)}y_s(z)\,dN_s(z). \tag{20}$$

4 | POTENTIAL APPLICATIONS

Due to its simplicity and generality, the model hands itself to a variety of applications useful for ecosystem management.

4.1 | Model calibration

Calibrating the model with empirical data makes it possible to understand which processes and factors play an important role in determining the ecosystem state. For the calibration, time series data of a characteristic state variable (or an index of the ecosystem state) and of important environmental conditions is required. After normalizing the conditions c_t to the interval $[0, 1]$, it is possible to fit the parameters of Equations (3) and (6) as well the functional relationship $\mu(c)$ using maximum-likelihood estimation. If the data exhibit abrupt regime shifts, knowledge about the threshold value μ_* across different conditions is required, which may be difficult to obtain in practice. In this case, it may be necessary to run an auxiliary model that includes higher power terms of X_t to identify all possible stable and unstable equilibria.

Once calibrated, the model may help in determining the relative importance of different factors (external driver, management action, random variation, rare event) that caused a regime shift. In a further step, one can quantify the extent to which different factors are responsible for a regime shift using the concept of partial responsibility (Baumgärtner, 2020; Vallentyne, 2008). We derive the probabilistic information required for this method in Section 4.4.

4.2 | Optimal management

Suppose the ecosystem manager faces the problem of maximizing expected intertemporal welfare derived from net benefits enjoyed from the ecosystem. These benefits, denoted by $\pi(r, a)$, depend on the chosen management action and differ between regimes. They consist of different levels of ecosystem services or direct economic benefits, such as harvest. Specifically, assume that the manager receives a flow of benefits $\pi_t(r_A, a) \neq \pi_t(r_B, a)$, irrespective of the precise level of the state variable X_t. Since the dynamic regimes are ultimately defined by the value of the state variable by (3), (5) and Definition 1, we rewrite the benefits as $\pi_t(X_t, a)$. The manager must choose a single management action a of type v, q or z at $t = 0$. She can choose from all feasible management actions described in Section 3.4, but incurs costs of $\kappa_t(a)$ associated with the action. We make no assumptions on the shape or time profile of $\kappa_t(a)$, other than it being a convex function. Social welfare is measured using a well-behaved utility function $U(\cdot)$, that is, $U'(\cdot) > 0, U''(\cdot) < 0$, and a time preference rate ρ. Hence, the manager needs to solve the problem

$$\max_a \mathbb{E}\left[\int_0^\infty \mathrm{e}^{-\rho t} U\left[\pi_t(X_t(a), a) - \kappa(a)\right] \mathrm{d}t\right] \tag{21}$$

subject to (15) and (17),

$$\pi_t(X_t, a) = \begin{cases} \pi_t(r_A, a) & \text{for } X_t \geq \mu_* \\ \pi_t(r_B, a) & \text{for } X_t < \mu_*, \end{cases} \tag{22}$$

and

$$X(0) = X_0(a);\ 0 \leq X_t \leq 1;\ c(0) = c_0;\ 0 \leq c_t \leq 1. \tag{23}$$

This problem cannot, in general, be solved analytically, but can be solved numerically (Kushner & Dupuis, 2001). In particular, the stochastic nature of the model dynamics suggests using dynamic programming techniques suited to deriving optimal feedback control rules rather than open-loop controls to account for uncertain system states (Bellman, 1966). This is an interesting decision problem with two trade-offs: the manager needs to choose not only the optimal intensity of the management action given costs and social risk and time preferences, but also the type of management action. In particular, there is an interesting choice along the temporal dimension between influencing the state variables or the conditions in the model (setting the option of management action z influencing the stochastic parameters momentarily aside). There is a trade-off between an immediate, but relatively short-lived intervention and a slow, persistent change. We would expect that the main factor influencing this decision is the size of the discount rate ρ. Larger values of ρ indicate a stronger time preference for the present and would imply taking management action v. Management action z will be optimal if the manager is very risk-averse.

4.3 | Viability management

Welfare-maximizing management based on discounted expected utility may not necessarily be sustainable in the sense that long-run costs and benefits tend to be neglected due to utility discounting (De Lara et al., 2015). In addition, economic analyses typically assume good substitutability between between natural and other forms of capital. This notion of weak sustainability (Neumayer, 2003) has been criticized for its inability to cope with multi-stability and other issues (van den Bergh, 2014). For these reasons, it may be preferable to use evaluation concepts that ensure strong sustainability under conditions of uncertainty and multi-stability, such as stochastic viability (Béné & Doyen, 2018; Doyen et al., 2019; Oubraham & Zaccour, 2018). The basic idea of stochastic viability is that the continued existence of certain ecosystem functions and components is guaranteed at all times with a sufficient probability (Baumgärtner & Quaas, 2009).

Under the stochastic viability approach an ecosystem manager needs to choose a management action from the set of *viable actions* a^{viab} which consists of those actions that are both admissible (a^{ad}) and that satisfy the state constraint of being above the threshold $X_t \geq \mu_*$ with at least the probability α:

$$a_\alpha^{\text{viab}}(X_0, t = 0) = \{a \in a^{\text{ad}} | P(X_t \geq \mu_*) \geq \alpha \ \text{ for all } \ t\}, \tag{24}$$

given the uncertain dynamics (15) and (17). The solution of this stochastic viability problem can be obtained with dynamic programming methods (Doyen & De Lara, 2010) that can readily be applied to our model.

4.4 | Probability of regime shift

The probability of flipping into an alternative regime is determined by the state variable's resilience to stochastic perturbations, which in our model is equivalent to the distance of the state variable X_t from its threshold value $\mu_*(c)$. The larger the resilience, the lower is the probability of a regime shift. For a known value of X_t at time t, we can calculate the *instantaneous* probability of a regime shift from r_A to r_B as the probability of the state variable X_t falling below its threshold value $\mu_*(c)$ within the next infinitesimal time interval dt:

$$\begin{aligned} P_t(r_A \rightarrow r_B | X_t) = P(\sigma \mathrm{d}W_t + y \leq -[X_t + \theta(\mu(c_{t+\mathrm{d}t}) - X_t) - \mu_*(c_{t+\mathrm{d}t})]) \cdot \lambda \mathrm{d}t \\ + P(\sigma \mathrm{d}W_t \leq -[X_t + \theta(\mu(c_{t+\mathrm{d}t}) - X_t) - \mu_*(c_{t+\mathrm{d}t})]) \cdot (1 - \lambda \mathrm{d}t), \end{aligned} \tag{25}$$

which explicitly considers the two possible cases of either a jump of random size y or no jump occurring. Since we have assumed independence of the three random variables, it is possible to use a single probability distribution for the sum $\sigma dW_t + y \sim \mathcal{N}(\bar{y}, \beta^2 + \sigma^2 dt)$.

This way of obtaining the probability of flipping into an alternative regime requires knowledge of the specific realization of the stochastic process X_t, which is known only once it has happened, or: ex post. In practice, today's management actions often affect the state of the system in the future and one needs to assess the probabilistic consequences of different actions before taking them, or: ex ante. In this case, one only knows the value of the state variable X_0 at time $t = 0$ and must form expectations about the state of the system at future points in time. In this case, it is possible to use the expected value and variance given in Equations (12) and (13) to calculate the expected instantaneous probability of regime shift at time t, assuming that no shifts have happened until that point in time.

There is a very simple, well-performing approximation of the expected probability of regime shift that is useful for management applications. The probability of a shift from regime r_A to regime r_B taking place at time t, conditional on having taken management action v at time 0 and no shifts having occurred until t, is approximately given by:

$$P_t(r_A \rightarrow r_B | \mathbb{E}[X_t(v)]) \approx p_t(v) = \bar{p}_t + \Delta p(v) \cdot \mathrm{e}^{-\theta t}, \tag{26}$$

where $\bar{p} = P_t(r_A \rightarrow r_B | \mathbb{E}[X_t])$ indicates the expected baseline probability of regime shift in the absence of management actions. The maximum change in probability due to the management action is denoted by $\Delta p(v)$ and needs to be calibrated. The approximation for management type q is very similar and given by:

$$P_t(r_A \rightarrow r_B | \mathbb{E}[X_t(q)]) \approx p_t(q) = \bar{p}_t + \Delta p(q) \cdot (1 - \mathrm{e}^{-\gamma t}). \tag{27}$$

Figure 7 shows the fit of the approximation to the actual, calculated probability. The probabilities due to action resemble simple exponential convergence and decay processes because by Equation (12), the expected ecosystem state responds exponentially with rate θ to changes in initial value (action v) and deterministic equilibrium value. The latter is determined by environmental conditions, which change exponentially (action q) with rate γ as given by Equation (17).

Due to the number of different parameters that may be affected by actions of type z, we do not provide a general approximation for management type z here.

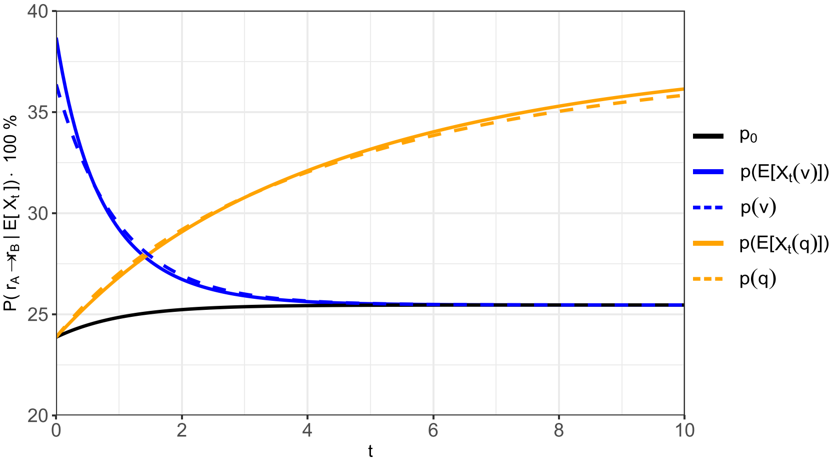

FIGURE 7 Regime shift probability over time for two types of management actions. Solid lines indicate calculated probabilities, dashed curves are approximations. Parameter values: $\nu = -25$, $\Delta p(\nu) = 0.125$, $q = 0.2$, $\Delta p(q) = 0.12$, $X_0 = 75$, $\mu_A(c_t) = 90 - 25c_t$, $\mu_*(c_t) = 80c_t$, $c_0 = 0.6$, $\gamma = 0.2$, $\theta = 1$, $\sigma = 5$, $\lambda = 0.3$, $\bar{y} = -10$, $\beta = 5$

A different and for some applications more useful way to assess the probability of regime shift is to calculate the probability of one shift within a time interval $[s, t]$ of arbitrary length. This is possible if the value of X_s at time s is known. The relevant time interval for ecosystem management based on probabilistic information is $[0, t]$. In the limit case of $[t, t + \mathrm{d}t]$, this reduces to the instantaneous probability of regime shift given by (25). More generally, the probability can be calculated for any s, t using the transition probability density function $P_t(X)$ of the stochastic process X_t. This density function can be obtained by solving the corresponding Fokker–Planck equation (in shorthand notation)

$$\frac{\partial P_t(X)}{\partial t} = \frac{\sigma^2}{2}\frac{\partial^2 P_t(X)}{\partial X^2} - \theta\mu\frac{\partial P_t(X)}{\partial X} + \theta\frac{\partial X P_t(X)}{\partial X} - \lambda P_t(X) + \lambda\int_0^\infty P_t(X - y)Q(y)dy, \qquad (28)$$

where $Q(y)$ is the probability distribution function of the jump size y. It is not possible to solve this equation analytically; numerical approximation methods are required to obtain the density function (Gaviraghi, 2017).

5 | DISCUSSION AND CONCLUSIONS

We have constructed a generic model of ecosystems with alternative stable states and stochastic dynamics, and their management. Our original contribution was to combine a novel deterministic multistability mechanism with two different stochastic influences: continuous diffusion and discrete jumps. Thus, we have improved the representation of stochasticity in models of ecosystems with alternative stable states. This provides a better understanding of the role of different deterministic and stochastic mechanisms and their interaction in causing regime shifts.

We now discuss limitations and potential extensions of the model. First, the model is formulated in terms of a single state variable to establish a clear focus on how stochasticity interacts with deterministic mechanisms of multistability. This neglects potential interactions between multiple state variables which may be relevant for some ecosystems. For some of these systems, it may be possible to construct an index of the ecosystem state (e.g., Blenckner et al., 2021), so that X_t is the index value at time t.

Second, the linearity of X_t in Equation (1) is seemingly at odds with the abrupt and nonlinear nature of regime shifts. The nonlinearity in our model arises from the bistability mechanism in Equation (3) which entails a discontinuous shift in the deterministic equilibrium $\mu(c)$ attracting the state variable. Hence, even though the response of the state variable to changes in its equilibrium value is linear, the overall system dynamics are nonlinear.[8]

Third, we assume that only the location of the deterministic equilibrium $\mu(c)$ changes when a regime shift occurs. We neglect that other parameters (listed in Table 1) could change as well. This is to focus on the core dynamic mechanism of alternative stable states. While it is plausible and easy to integrate in the model that other parameters change, this would not qualitatively change the dynamics of regime shifts.[9]

Last, in our model the uncertainty regarding the dynamics of the ecosystem is probabilistic. That is, we assume perfect knowledge about the distribution of stochastic perturbations and no fundamental uncertainties regarding the location of thresholds, consequences of management actions, or values of model parameters. Essentially, our model is rich in environmental *risk*, but assumes a high degree of knowledge. Depending on the specific system under study, consideration of deeper forms of uncertainty might be needed. This would require a completely different approach to modeling.

With these limitations and reservations in mind, applying the model to ecosystems with alternative stable states as outlined in Section 4 opens new pathways for assessing management when stochastic influences are important.

AUTHOR CONTRIBUTIONS

Michael Stecher: conceptualization (equal), formal analysis (lead), methodology (lead) software (lead), visualization (lead), writing – original draft (lead), writing – review & editing (equal). **Stefan Baumgärtner:** conceptualization (equal), funding acquisition (lead), methodology (supporting), supervision (lead), writing – review & editing (equal)

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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ENDNOTES

[1] Bifurcation points are also referred to as "tipping points" (e.g., Dakos et al., 2019) or "thresholds" (e.g., May, 1977). A discussion of the terminology is given by van Nes et al. (2016). To avoid confusion, we stick to the technical term and use the word threshold only for unstable equilibria between basins of attraction.

[2] In the clear and turbid regimes, the equilibrium transparency of the lake water changes only slightly across a wide range of nutrient levels—the overall structure and characteristic state of the lake (whether it is clear or turbid), as well as the feedbacks stabilizing it, remain unchanged within a dynamic regime.

[3] A similar definition of the ability to withstand shocks is called *resistance* by Harrison (1979) and Grafton et al. (2019).

[4] A minimal mathematical model of the dynamics described in this section can be formulated as $\mathrm{d}x/\mathrm{d}t = l - bx + x^k/(x^k + h^k)$, where x is the state variable, l is a factor that promotes x, b and r are the rates at which x decays and recovers, and h is a threshold at which the last term increases steeply, with the steepness determined by k. For the exemplary case of shallow lakes, x are suspended nutrients, l is nutrient loading, b is the nutrient removal rate and r represents internal nutrient recycling (Scheffer et al., 2001).

[5] The O–U process was originally introduced by Uhlenbeck and Ornstein (1930) to model the velocity of a Brownian particle.

[6] In fact, the rate of change of environmental conditions can be several orders of magnitude slower than the rate of change of state variables (Rinaldi & Scheffer, 2000). For instance, even though the current rate of accumulation of greenhouse gases in the atmosphere is unprecedented in geological history, the resulting changes in climatic conditions unfold relatively slowly compared to the changes in population densities or species abundances they entail.

[7] Formally, in Equations (6), (10), (12), and (15), c is time-dependent according to (17); and in Equation (14) $\mu(c)$ is replaced by $\mu(c_0 + \Delta c)$.

[8] In cases where the response of the state variable to changes in its equilibrium value is nonlinear, one can linearize the dynamics around the equilibrium using a first-order Taylor approximation. That is, one may approximate some nonlinear dynamics $F(X_t, c)$ around the equilibrium $X_t = \mu(c)$ so that $F(X_t, c) \approx F_X(\mu(c), c) \cdot (X_t - \mu(c))$.

[9] For instance, if discontinuous jumps represent fire disturbances in a savannah, the jump parameters $\lambda, \bar{y}$ and β should depend on the vegetation regime to consider fuel available for fires (D'Odorico et al., 2006).

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APPENDIX A: MATHEMATICAL DERIVATIONS

Solution of Equation (6)

Starting with the stochastic differential equation

$$dX_t = \theta(\mu(c) - X_t)dt + \sigma dW_t + ydN_t, \tag{A1}$$

we employ the method of variation of parameters by setting $Y_t = X_t \mathrm{e}^{\theta t}$. Employing Itô's Lemma and the chain rule of differentiation we get:

$$\begin{aligned} dY_t &= \theta X_t \mathrm{e}^{\theta t} dt + \mathrm{e}^{\theta t} dX_t \\ &= \theta X_t \mathrm{e}^{\theta t} dt + \mathrm{e}^{\theta t}[\theta(\mu(c) - X_t)\mathrm{d}t + \sigma dW_t + ydN_t] \\ &= \mathrm{e}^{\theta t}\theta\mu(c)dt + \mathrm{e}^{\theta t}\sigma dW_t + \mathrm{e}^{\theta t} ydN_t. \end{aligned} \tag{A2}$$

Integrating from 0 to t and using the initial value $Y_{t=0} = Y_0 = X_{t=0}\mathrm{e}^{\theta t} = X_0 \mathrm{e}^{\theta t}$, we obtain:

$$Y_t = [\mathrm{e}^{\theta t}\mu(c)]_0^t + \sigma\int_0^t \mathrm{e}^{\theta s} dW_s + \int_0^t \mathrm{e}^{\theta s} y_s dN_s + K. \tag{A3}$$

Seeing that for $t = 0, K = Y_0$, we write:

$$Y_t = Y_0 + \mu(c)(\mathrm{e}^{\theta t} - 1) + \sigma\int_0^t \mathrm{e}^{\theta s} dW_s + \int_0^t \mathrm{e}^{\theta s} y_s dN_s. \tag{A4}$$

Transforming back with $X_t = Y_t \mathrm{e}^{-\theta t}$, we get the solution in terms of stochastic integrals which is given in the main text:

$$X_t = X_0 \mathrm{e}^{-\theta t} + \mu(c)(1 - \mathrm{e}^{-\theta t}) + \sigma\int_0^t \mathrm{e}^{\theta(t-s)} dW_s + \int_0^t \mathrm{e}^{\theta(t-s)} y_s dN_s. \tag{A5}$$

Expected value of jumps

The expected value of the last term of (A5) is obtained as follows:

$$\begin{aligned} \mathbb{E}_{y,\mathrm{d}N}\left[\int_0^t \mathrm{e}^{-\theta(t-s)} y_s dN_s\right] = \quad & \bar{y}\,\mathbb{E}_{\mathrm{d}N}\left[\int_0^t \mathrm{e}^{-\theta(t-s)} dN_s\right] \\ &= \bar{y}\int_0^t \mathrm{e}^{-\theta(t-s)}\lambda ds = \bar{y}\left[\frac{1}{\theta}\mathrm{e}^{-\theta(t-s)}\lambda\right]_0^t \\ & \bar{y}\left[\frac{\lambda}{\theta} - \frac{\lambda}{\theta}\mathrm{e}^{-\theta t}\right] = \bar{y}\,\frac{\lambda}{\theta}(1 - \mathrm{e}^{-\theta t}). \end{aligned} \tag{A6}$$

To check whether this expression increases or decreases in θ take the derivative with respect to θ:

$$\frac{\partial}{\partial\theta}\bar{y}\,\frac{\lambda}{\theta}(1-\mathrm{e}^{-\theta t}) = -\,\bar{y}\,\frac{\lambda}{\theta^2}+\bar{y}\,\frac{\lambda}{\theta^2}\mathrm{e}^{-\theta t}+\bar{y}\,\frac{\lambda}{\theta}t\mathrm{e}^{-\theta t} = -\,\bar{y}\,\frac{\lambda}{\theta^2}+\bar{y}\,\frac{\lambda\mathrm{e}^{-\theta t}(\theta t+1)}{\theta^2}. \tag{A7}$$

Whether this derivative is positive or negative depends on the sign of $\bar{y}$. For $\bar{y} > 0$, the derivative is negative, for $\bar{y} < 0$ it is positive. That is, the derivative will be negative if:

$$\bar{y}\,\frac{\lambda}{\theta^2} > \bar{y}\,\frac{\lambda\mathrm{e}^{-\theta t}(\theta t+1)}{\theta^2}. \tag{A8}$$

For $\bar{y} > 0$, we have that

$$\begin{aligned} 1 &> \mathrm{e}^{-\theta t}(\theta t+1)\\ \mathrm{e}^{\theta t} &> \theta t+1, \end{aligned} \tag{A9}$$

which holds by the power series definition of the exponential function for all $t > 0$ (since $\theta > 0$ by assumption):

$$e^{\theta t} = 1+\theta t+\frac{(\theta t)^2}{2!}+\frac{(\theta t)^3}{3!}+\cdots > 1+\theta t. \tag{A10}$$

For $\bar{y} < 0$, all inequality signs are reversed and the modified form of (A9) does not hold. The proof for the opposite case of (A7) <0 is analogous.