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Probabilistic measures for biological adaptation and resilience

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This paper introduces an approach to quantifying ecological resilience in biological systems, particularly focusing on noisy systems responding to episodic disturbances with sudden adaptations. Incorporating concepts from nonequilibrium statistical mechanics, we propose a measure termed "ecological resilience through adaptation," specifically tailored to noisy, forced systems that undergo physiological adaptation in the face of stressful environmental changes. Randomness plays a key role, accounting for model uncertainty and the inherent variability in the dynamical response among components of biological systems. Our measure of resilience is rooted in the probabilistic description of states within these systems and is defined in terms of the dynamics of the ensemble average of a model-specific observable quantifying success or well-being. Our approach utilizes stochastic linear response theory to compute how the expected success of a system, originally in statistical equilibrium, dynamically changes in response to a environmental perturbation and a subsequent adaptation. The resulting mathematical derivations allow for the estimation of resilience in terms of ensemble averages of simulated or experimental data. Finally, through a simple but clear conceptual example, we illustrate how our resilience measure can be interpreted and compared to other existing frameworks in the literature. The methodology is general but inspired by applications in plant systems, with the potential for broader application to complex biological processes.

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I. INTRODUCTION

Resilience refers to the ability of a system to maintain a certain degree of functionality in the face of disturbances [1]. In the seminal work by Holling [2,3], resilience is conceptually categorized as "engineering" or "ecological." In engineering resilience, perturbations are small and the system returns to an original equilibrium state. Ecological resilience, however, applies to systems with multiple equilibria and perturbations that can induce the system to move between different attractors. Our focus is ecological resilience, in particular applied to biological systems that operate out of equilibrium and that respond by sudden adaptations as a result of episodic disturbances.

Multiple quantitative resilience measures have been proposed for living systems based upon dynamical systems theory, including linear stability of equilibria, return times, attractor size and geometry, distance to bifurcation manifolds, elasticity, and hysteresis in response to different types of perturbations: pulses, presses, ramps, deterministic, and stochastic. See Dakos and Kéfi [1], Angeler and Allen [4], Yi and Jackson [5], Van Meerbeek *et al.* [6] for useful reviews. These measures receive often interchangeable names as resilience, resistance, robustness, stability, recovery, malleability, and tolerance. Altogether, these quantities can help understand how living systems adjust, recover or heal after perturbations, and account for the degree to which they return back to an unperturbed state or to transition to another metastable but viable operating point.

The mathematical framework of preference for quantifying resilience has been the theory of dynamical systems as in Guckenheimer and Holmes [7], Krakovská *et al.* [8], Arnoldi *et al.* [9], with random perturbations by Refs. [10,11], or in networked systems by Refs. [12,13]. Here we argue that ecological resilience can be better achieved by conceptualizing the systems of interest as noisy/forced systems, applying the techniques that occupy the attention of nonequilibrium statistical mechanics. Such a probabilistic framework will be conducive to a notion of ecological resilience that emphasizes persistence and reflects the opportunistic and unpredictable aspects of change in biological systems. It will measure the degree to which a system can adapt to a perturbation by controlling its behavior to increase the probabilities of not falling into a state of low well-being.

Our argument is based on the observation that the temporal evolution of observable biological quantities is rich with noise as a result of the inherent uncertainty in observables and the variability among individuals, or more generally, subsystems. It also incorporates the epistemic error associated with incomplete or uncertain model parametrizations. Therefore a system's ability to adjust its function to disturbances can be conceptualized in terms of the effect of the perturbation over the probability distribution of states and the expected value

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of some measure of well-being. Employing a probabilistic description of these observables allows for a more nuanced understanding of these systems, particularly in describing the living states and behavior that extend beyond the realm of deterministic dynamics.

We propose a measure of *ecological resilience through adaptation* applicable to noisy, forced systems undergoing environmental perturbations. The goal is to provide a mathematical framework in which the dynamic response of the system to perturbation can be quantified, either from ensembles of models or data realizations. Specifically, we provide a probabilistic measure of the degree to which a system in statistical equilibrium can dynamically adapt, recover, or change equilibrium distribution after an stressful perturbation on the parameters modeling its environmental conditions. Here, we use the word "adaptation" in the physiological sense, namely as the ability of living systems to adjust their dynamics (e.g., metabolism) in response to its changing environment. The degree of "recovery" is conceptualized in terms of a *success function* of the state variables designed to model performance, health, productivity; it is an arbitrary measure of well-being that the modeler seeks to maintain as high as possible in average for any given environmental conditions. The probabilistic approach allows, not only for dynamic models of aleatoric, epistemic or measurement uncertainty (e.g., observations and parameters in stochastic differential equations), but also to assess resilience of an aggregate or ensemble of subsystems exhibiting random variations on their state variables.

Our formulation uses modern methods in stochastic process theory to capture changes in the probabilistic distribution of the state of a forced/noisy systems that is dynamically perturbed. Specifically, we rely on *linear response theory* to predict how the expected value of the success function changes in response to environmental disturbances and physiological adaptations. This approach has firm foundations for both deterministic chaotic dynamical systems [14] and their stochastic counterpart [15]. Indeed, linear response theory allows us to compute the system's response to disturbances using response operators acting on the unperturbed system, hence our framework provides practical ways of designing ensemble experiments from which resilience through adaptation can be estimated.

Important insights into the intricacies of the effect of disturbances to complex systems have been elucidated through linear response theory. For example, Held and Kleinen [16], Lenton *et al.* [17] showed that the divergence of the response operator occurs in the proximity of a system to critical behavior due to bifurcations. Moreover the presence of very high sensitivity to perturbations has been showed to be connected to the presence of the so-called critical slowing down, i.e., the presence of slow decay of correlations [see 18,19]. As shown in Refs. [19,20] both phenomena are due to the near-prevalence of positive, destabilizing feedbacks over the negative, stabilizing ones. In other words, adaptation can be slow and inefficient, which reduces the overall system's resilience.

In the context of ecological resilience, to the best of our knowledge, this is the first study that applies linear response theory to perturbations on noisy forced systems. In fact, very few articles have considered ecological resilience for stochastic systems. The stochastic model of Arnoldi *et al.* [9], for example, treats noise as the source of perturbation to a linear deterministic system and quantifies resilience as the degree of stochastic variability around the equilibrium point. This type of analysis, which we call *path resilience* is not the focus of the present study. For us, noise is a fundamental component of the dynamics, and we consider structural perturbations, namely changes to the model parameters. The work of Ref. [21] shares some similarities with our work but is much more limited in scope. There, the author investigates the response of populations interacting via a particular logistic model to perturbations on intrinsic growth rates. Resilience in Ref. [21] is not measured with respect to adaptation, but as a change of the population's statistical variability per unit perturbation.

This article focuses on the conceptual and mathematical basis of ecological resilience rather than on the intricacies of a given model. The formulation is quite general but inspired by applications to the quantification of resilience of living systems, in particular plants and, in principle, should be generalizable to complex systems comprising multiple biological processes. Throughout, we highlight along the mathematical derivations those concepts or processes of plant resilience that could be modeled by our framework, although application to real plant-system models is left for future work. For illustration, we use a simple bifurcating stochastic differential equation to exemplify our notion of resilience, as to not be encumbered by the complexities of a natural system.

The organization is as follows. In Sec. II, we describe the model that conceptualizes the dynamics of observables. These observables are described as time dependent multidimensional probabilistic distributions associated with the organism function. Section III introduces our measure of resilient adaptation along with a comparative analysis contrasting our proposal with existing methods. In Sec. IV we carry out the process of quantifying the resilience to adaptation to a simple and familiar stochastic dynamics problem described by a Langevin equation. Finally, in Sec. V we summarize the proposed measure of resilience to adaptation measure and discuss the assumptions and conditions required for its applicability.

II. PRELIMINARIES

We now describe the mathematical framework upon which ecological resilience through adaptation is formulated. Our focus is on the temporal dynamics of a state variable $X(t) \in \mathbb{R}^N$ representing chemical and/or physical variables within a living system. In the case of plant physiology these could be the variables involved in a photosynthesis model (e.g., water potential, carbohydrate concentrations or flows, chlorophyl, stomata aperture). We will also assume that there are identifiable environmental stressors $\epsilon \in \mathbb{R}^P$ (e.g., solar radiation, ambient temperature, ambient or soil moisture) that have known or measurable effects on the dynamics of X. The variables that take on the role of adaptation variables also appear as parameters in the dynamics of X. We label the adaptation variables by $\alpha \in \mathbb{R}^Q$. Our theoretical model for the evolution of the observable subset of the state variables is a stochastic differential equation [22] of the form

$$dX = F_{\epsilon,\alpha}(X)\,dt + \sigma\,dW_t, \quad t > 0, \quad X(0) \sim p_0. \tag{2.1}$$

The drift term $F_{\epsilon,\alpha} \in \mathbb{R}^N$ is known for constant values of ϵ and α. The incremental Wiener processes dW_t has the same dimensions as $F_{\epsilon,\alpha}$. The assumed constant $\sigma \in \mathbb{R}^{N\times N}$ is a nonnegative symmetric noise amplitude matrix.

Model (2.1) includes two sources of variability in the dynamics of X: for any fixed initial starting condition $X(0)$, an infinite amount of $X(t)$ histories can be generated (each corresponding to a realization of W), reflecting the random/noisy nature of the differential equation itself due to aleatoric or epistemic error. The other source of variability is encoded in the initial conditions: To model subsystem variability, we will assume that $X(0)$ is taken from a known probability distribution p_0 over $\mathbb{R}^N$. This aspect of the model accommodates for variability in the biological system itself (e.g., variability in leaves of the same plant).

The function $F_{\epsilon,\alpha}$ encodes all the known deterministic regulatory dynamics of the system. The noise represents random fluctuations that are present in the dynamics of X and are modeled by an additive diffusion process which, in this work, are assumed independent of ϵ and α although the analysis can be naturally extended. For current plant function models at leaf scale [see Refs. 23,24, for example] the state variable has dimension $N \sim 10$ and include concentrations and fluxes important for carbon assimilation and transpiration, as well as vascular transport. The environmental variables ϵ are fewer and determine atmospheric and soil boundary conditions. The distinction between the adaptation parameters in α and the state variables in X is more subtle. Typically, α includes regulatory or control variables whose dynamics are left out of Eq. (2.1), because they operate at different length scales, are poorly understood, or can be deliberately changed in experiments. In the case of plants experiencing water deficit, for example, regulatory variables include the concentration abscisic acid, ions of calcium and potassium, and stomatal aperture [25].

To emphasize the dependence of the system on the parameters, we denote by $X_{\epsilon,\alpha} = \{X_{\epsilon,\alpha}(t) : t \geqslant 0\}$ the solution to Eq. (2.1) for constant values of ϵ and α. The key to our proposal is the mean evolution of observables of the process, namely expectations of the form $\mathbb{E}S(X_{\epsilon,\alpha}(t))$ where $S : \mathbb{R}^N \to \mathbb{R}$ is some measure of success or well-being to be discussed further below. For now, in what follows, we explain the mathematical notation and background required for estimating the response of $\mathbb{E}S(X_{\epsilon,\alpha}(t))$ to changes in ϵ and α, in terms of linear response theory. For details see Ref. [22].

We suppose that that the drift $F_{\epsilon,\alpha}(x)$ in Eq. (2.1) is sufficiently smooth as a function of the state variable x so that the strong solution to Eq. (2.1) is a diffusion process. We also assume that $F_{\epsilon,\alpha}$ is differentiable with respect to the parameters ϵ and α. For simplicity, we also suppose that the noise amplitude matrix is diagonal and isotropic $\sigma = \sigma I_N$ for some $\sigma > 0$. The process $X_{\epsilon,\alpha}$ has an infinitesimal generator

$$\mathcal{L}_{\epsilon,\alpha}[S] = F_{\epsilon,\alpha} \cdot \nabla S + \frac{\sigma^2}{2}\nabla^2 S, \tag{2.2}$$

for all functions S in the domain $\mathrm{Dom}(\mathcal{L}_{\epsilon,\alpha})$ which is supposed to be independent of ϵ or α, and dense within a Banach space $\mathcal{B}(\mathbb{R}^N)$. The operator $\mathcal{L}_{\epsilon,\alpha}$ determines the evolution of the semigroup

$$\mathbb{E}_x\, S(X_{\epsilon,\alpha}(t)) = e^{t\mathcal{L}_{\epsilon,\alpha}}[S](x), \quad t \geqslant 0 \tag{2.3}$$

for all $S \in \mathrm{Dom}(\mathcal{L}_{\epsilon,\alpha})$. The subscript x in the expectation denotes conditioning on the initial value $X_{\epsilon,\alpha}(0) = x$. For $\lambda > 0$, we denote by $\mathcal{R}^{(\lambda)}_{\epsilon,\alpha}$ the resolvent operator of $\mathcal{L}_{\epsilon,\alpha}$. Namely,

$$\mathcal{R}^{(\lambda)}_{\epsilon,\alpha}[S] = (\lambda - \mathcal{L}_{\epsilon,\alpha}[S])^{-1} = \int_0^\infty e^{-\lambda t} e^{t\mathcal{L}_{\epsilon,\alpha}}[S]\,dt, \tag{2.4}$$

for any $S \in \mathrm{Dom}(\mathcal{L}_{\epsilon,\alpha})$. The adjoint to Eq. (2.2) is the Fokker-Planck operator

$$\mathcal{L}^*_{\epsilon,\alpha}[p] = -\nabla\cdot(pF_{\epsilon,\alpha}) + \frac{\sigma^2}{2}\nabla^2 p. \tag{2.5}$$

For an initial distribution p_0, the probability distribution $p_{\epsilon,\alpha}(t,x)$ of $X_{\epsilon,\alpha}(t)$ conditional to $X_{\epsilon,\alpha}(0) \sim p_0$ evolves according to the "forward equation,"

$$\frac{\partial p_{\epsilon,\alpha}}{\partial t} = \mathcal{L}^*_{\epsilon,\alpha}[p_{\epsilon,\alpha}], \quad p_{\epsilon,\alpha}(0) = p_0, \tag{2.6}$$

namely $p_{\epsilon,\alpha}(t) = e^{t\mathcal{L}^*_{\epsilon,\alpha}}[p_0]$. Hence, expectations of an observable can be computed as

$$\mathbb{E}_{p_0}\, S(X_{\epsilon,\alpha}(t)) = \int_0^t S(x) e^{s\mathcal{L}^*_{\epsilon,\alpha}}[p_0](x)\,ds \tag{2.7}$$

for any bounded $S : \mathbb{R}^N \to \mathbb{R}$. Last, we will assume that for all ϵ, α of interest, the diffusion $X_{\epsilon,\alpha}$ is ergodic with unique invariant probability $\bar{p}_{\epsilon,\alpha}$. Namely, $\mathcal{L}^*_{\epsilon,\alpha}[\bar{p}_{\epsilon,\alpha}] = 0$ and expectations can be computed as

$$\begin{aligned}\lim_{t\to\infty} \mathbb{E}_x(S(X_{\epsilon,\alpha}(t))) &= \mathbb{E}_{\bar{p}_{\epsilon,\alpha}}(S(X_{\epsilon,\alpha}(t)))\\ &= \int S(x)\bar{p}_{\epsilon,\alpha}(x)\,dx =: \bar{S}_{\epsilon,\alpha}\end{aligned} \tag{2.8}$$

for all $t \geqslant 0$ and $x \in \mathbb{R}^N$, which amounts to assuming that for any ensemble described by p_0, the process $X_{\epsilon,\alpha}(t)$ asymptotically converges in probability to the invariant measure $\bar{p}_{\varepsilon,\alpha}$.

III. RESILIENT ADAPTATION

We will propose a measure of resilience aimed at quantifying the ability of the system to adapt through changes on α, to environmental disturbances on ϵ that are stressful with respect to some measure of performance, well-being, productivity, or success.

A. Background

It is common to consider the resilience of deterministic homeostatic systems evolving along a stability landscape. Namely, a model of the form $dX/dt = F_{\epsilon,\alpha}(X)$ where $F_{\epsilon,\alpha} = -\nabla V_{\epsilon,\alpha}$ and $V_{\epsilon,\alpha}$ is a potential surface.. Resilience is studied by perturbing the state X away from a stable equilibrium and analyzing its homeostatic relaxation to the same or other stable equilibria [see Refs. 1,6].

The noisy case presented in Eq. (2.1) has been widely studied in nonequilibrium statistical mechanics literature as a model of a system evolving towards a potential energy minimum with random fluctuations (see Refs. [22,26], for example). The paths of X do not necessarily converge to equilibrium states, but will actually transition randomly between attractors due to the combination of noise or forcings. This stochastic homeostatic behavior has been used by Meyer [10], Arani *et al.* [11], Krakovská *et al.* [8] and others to study what we call "path-wise resilience" to random perturbations. Namely, paths generated from any initial state drift towards the neighborhood of the local minima of $V_{\epsilon,\alpha}$ just as in the deterministic case, but are continuously subjected to random fluctuations whose magnitude depend on the amplitude σ of the noise process. If σ is sufficiently large, or enough time passes, then these fluctuations will drive paths across any unstable equilibrium into another basin of attraction where the system will recover in a different homeostatic state. In fact, estimates for the probability of such changes and the average time they take are well-known for the dynamics given by Eq. (2.1) and are described in the weak-noise limit by large deviation laws [11,27,28]. This, however, is not our focus. We are interested in structural resilience with respect to parameter changes, and on the average over all possible paths.

In contrast with the two approaches described above, we regard biological systems as *homeodynamic* and assume that they can transform their dynamics through behavioral changes in response to perturbations [29]. We refer to this behavioral changes as adaptations and model them as changes $\alpha \to \alpha + \Delta\alpha$ in response to environmental perturbations of the form $\epsilon \to \epsilon + \Delta\epsilon$. The homeodynamic response, when described in terms of temporally dependent distributions, can be analyzed using linear response theory. Specifically, we can obtain first order estimates to the sensitivity of the expectation of key observables associated with the perturbations $\Delta\epsilon$ and $\Delta\alpha$.

Further, we conceptualize ecological resilience in terms of a *success function* $S : \mathbb{R}^N \to [0,\infty)]$; an observable that measures well-being, fitness, productivity, etc., as a function of the system state $X_{\epsilon,\alpha}(t)$ at any given time, and under specific operating conditions determined by parameters ϵ and α. States x for which $S(x)$ is close to zero are associated with biological stress. For example, in plants, S could represent photosynthetic output under various environmental conditions. Mathematically, we assume S is a bounded function belonging to $\mathrm{Dom}(\mathcal{L}_{\epsilon,\alpha})$ for all values of interest of ϵ, α.

This study focuses on the dynamics of the mean of $S(X_{\epsilon,\alpha}(t))$ rather than the potentially complex and high-dimensional sample paths of $X_{\epsilon,\alpha}(t)$. Specifically, resilience is quantified in terms of how the average success, expressed as $\mathbb{E}S(X_{\epsilon,\alpha}(t))$, reacts to changes to ϵ and α. The expectation here is meant as an ensemble mean over a large group of individuals or subsystems.

B. Perturbation, adaptation, and resilience

The solution $X_{\epsilon,\alpha}$ to Eq. (2.1) represents the dynamics of the system under constant environmental and metabolic conditions. In the context of resilience we are interested in the ensemble properties of the solution under changing values of ϵ and adaptations of α. Specifically, we consider a process X defined by the following three steps: For $t < 0$ the system is evolving in probabilistic equilibrium under the operation conditions (ϵ_0, α_0), namely $X(t) \sim \bar{p}_{\epsilon_0,\alpha_0}$ for all $t < 0$. At $t = 0$ a sudden environmental disturbance $\epsilon_0 \to \epsilon_1$ occurs. After a random time $\tau \sim \exp(\lambda)$ the system adapts by switching $\alpha_0 \to \alpha_1$. See Fig. 1. For $t \geqslant 0$ the resulting process can be described as

$$X(0) \sim \bar{p}_{\epsilon_0,\alpha_0}, \qquad X(t) = \begin{cases} X_{\epsilon_1,\alpha_0}(t) & 0 < t \leqslant \tau, \\ X_{\epsilon_1,\alpha_1}(t) & t > \tau, \end{cases} \tag{3.1}$$

where the continuity condition $X_{\epsilon_1,\alpha_0}(\tau^-) = X_{\epsilon_1,\alpha_1}(\tau^+)$ is assumed to hold with probability one.

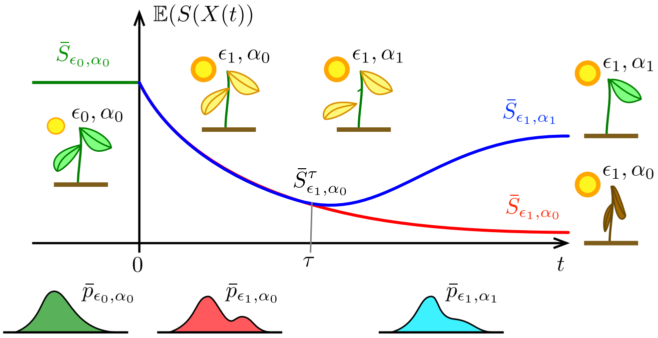

FIG. 1. Schematic representation of the evolution of the expected success $\mathbb{E}S(X(t))$ for X given by Eq. (3.1). For $t < 0$ the system is in statistical equilibrium under $\bar{p}_{\epsilon_0,\alpha_0}$. At $t = 0$ the perturbation $\epsilon_0 \to \epsilon_1$ occurs (e.g., temperature increases) and $S(X(t))$ starts decreasing in average. If no adaptation takes place, then the red curve is followed towards the equilibrium distribution $\bar{p}_{\epsilon_1,\alpha_0}$. Adaptation occurs at the random time τ and the resilient system recovers to the equilibrium distribution $\bar{p}_{\epsilon_1,\alpha_1}$.

Note that the adaptation $\alpha_0 \to \alpha_1$ is assumed to occur instantaneously at a random "reaction time" τ representing the time it takes for the regulatory signals to take effect. Randomness here means that each individual suffering the disturbance might react at a different time, but in the ensemble, these times follow the prescribed exponential distribution with mean $1/\lambda$ units of time. This modeling assumption can be interpreted as consistent with a case in which the underlying adaptation dynamics $d\alpha = g(\epsilon, X)\,dt$ are poorly understood or deliberately left out of the model (2.1), or unresolved at the timescales of t. The choice of the exponential distribution for τ is parsimonious, and has the mathematical advantage of making X a Markov process.

We are interested in the dynamical behavior of the ensemble mean $\mathbb{E}(S(X(t))$ of the success throughout the sequence of invariance-perturbation-adaptation. For constant ϵ, α we denote by $\bar{S}_{\epsilon,\alpha}$ the mean of S under the invariant distribution $\bar{p}_{\epsilon,\alpha}$, i.e., Eq. (2.8). Note that by the construction of X,

$$\mathbb{E}(S(X(0)) = \bar{S}_{\epsilon_0,\alpha_0}, \qquad \lim_{t\to\infty} \mathbb{E}(S(X(t)) = \bar{S}_{\epsilon_1,\alpha_1}. \tag{3.2}$$

In the context of resilience we study the trajectory in time of the ensemble average of the success between the extremes in Eq. (3.2). See Fig. 1.

Concepts related to resilience to parameter disturbances are usually defined with respect to the initial, worst, and final states of an observable during the process of perturbation/response/recovery. See, for example, Refs. [5,6]. In the context of the time evolution of the expected success, the usual framework proposes the following definition of resilience:

$$R = \frac{\bar{S}_{\epsilon_1,\alpha_1} - \min_{t\geqslant 0} \mathbb{E}(S(X(t))}{\bar{S}_{\epsilon_0,\alpha_0} - \min_{t\geqslant 0} \mathbb{E}(S(X(t))}, \tag{3.3}$$

which in Ref. [5] is called "recovery," and equals one minus "recovery capacity" over "resistance" in the notation of Ref. [6].

One drawback of the definition III.3 is that the term $\min_{t\geqslant 0} \mathbb{E}(S(X(t))$ is not an ensemble average. Furthermore, its computation requires estimation of $\mathbb{E}S(X(t))$ at all times. To address this, we exploit the assumption of the existence of a population-wide reaction time with known probability distribution and define "resilience adaptation" as follows.

Definition III.1. Let X be the solution to Eq. (3.1), S the success function and τ the adaptation time. Denote $\bar{S}^{\tau}_{\epsilon_1,\alpha_0} := \mathbb{E}S(X(\tau))$. Then the resilience of X to the perturbation $\epsilon_0 \to \epsilon_1$ and through the adaptation $\alpha_0 \to \alpha_1$ is

$$R_\tau = \frac{\bar{S}_{\epsilon_1,\alpha_1} - \bar{S}^{\tau}_{\epsilon_1,\alpha_0}}{\bar{S}_{\epsilon_0,\alpha_0} - \bar{S}^{\tau}_{\epsilon_1,\alpha_0}}. \tag{3.4}$$

We will argue that R_τ is a practical and informative measure of ecological resilience, and that is consistent with existing methodologies.

C. Computing and interpreting resilience

The resilience R_τ in Eq. (3.4) can be any real number and has the following interpretation:

(1) A value $0 < R_\tau < 1$ measures the fraction of the success that the system was able to recover with the adaptation, with respect to the total loss of success due to the disturbance.

(2) A value $R > 1$ indicates a very resilient system, in which the long-term success after the adaptation $\bar{S}_{\epsilon_1,\alpha_1}$ is larger than the initial $\bar{S}_{\epsilon_0,\alpha_0}$.

(3) In the case of stressful environmental perturbations, where $\bar{S}_{\epsilon_0,\alpha_0} > \bar{S}^{\tau}_{\epsilon_1,\alpha_0}$, R_τ is negative only if the adaptation $\alpha_0 \to \alpha_1$ is also detrimental with respect to the mean state of the system when the adaptation occurs.

With respect to the usual definition or resilience R in Eq. (3.3), we note that is not equal to R_τ in general, although the example in Sec. IV shows that it can be a good approximation. We argue, however, that R_τ is a more practical measure of ecological resilience than R because can be computed in terms only of averages. The main argument stems from the fact that while $\min \mathbb{E}S(X(t))$ is a deterministic ensemble diagnostic, the reaction time τ pertains to the physiological ability of the system to adapt or heal, and is hence a random variable that can be modeled. This, as described below, opens up several possibilities for computation of R_τ.

The usual resilience R can be, in principle, computed from experiments that involve the comprehensive monitoring of a large population. In such an experiment, up to Gaussian errors, each individual must be subjected to the same environmental disturbance $\epsilon_0 \to \epsilon_1$ and react with the (possibly unknown) adaptation $\alpha_0 \to \alpha_1$ that has measurable effects on the success throughout time. The average of S must be computed at enough times to discern the minimum value of $\mathbb{E}S(X(t))$. In this experimental context, computing R_τ might not be very practical because estimating $\bar{S}^{\tau}_{\epsilon_1,\alpha_0}$ would require measuring S on each individual at the exact moment it adapts. However, if a model for the dependence of X on ϵ and α as in Eq. (3.1) is available, then R_τ is a more practical measure than R because it can be estimated from an ensemble of simulations of fixed dynamics under fixed initial distributions.

Furthermore, note that by Eq. (3.1), we can write $\bar{S}^{\tau}_{\epsilon_1,\alpha_0}$ by taking expectations jointly over τ and the paths of X_{ϵ_1,α_0} conditioned on $X_{\epsilon_1,\alpha_0}(0) \sim \bar{p}_{\epsilon_0,\alpha_0}$. This yields the following expression in terms of the resolvent [see Eq. (2.4)]:

$$\begin{aligned}\bar{S}^{\tau}_{\epsilon_1,\alpha_0} &= \mathbb{E}_{\bar{p}_{\epsilon_0,\alpha_0}}[S(X_{\epsilon_1,\alpha_0}(\tau))]\\ &= \lambda \int \mathcal{R}^{(\lambda)}_{\epsilon_1,\alpha_0}[S](x)\, \bar{p}_{\epsilon_0,\alpha_0}(x)\, dx.\end{aligned} \tag{3.5}$$

Hence, if a model $F_{\epsilon,\alpha}$ is at hand and the operator $\lambda - \mathcal{L}_{\epsilon,\alpha}[S]$ can be analytically or numerically inverted, then one can estimate $\bar{S}^{\tau}_{\epsilon_1,\alpha_0}$ only from observations or simulations of the unperturbed system. This feature is key, as we will demonstrate in Sec. III D, it yields useful estimation methods for R_τ.

Our proposal R_τ can be related to other resilience measures applicable to noisy systems. First, in Ives [21], resilience is measured with respect to perturbations that increase the variability of a dynamically evolving population. Namely, the variance of $X(t)$ is used as a an inverse metric of success. Although the analysis in Ives [21] is limited to the rate of increase of the variance after an environmental perturbation, we can write the definition (III.1) with respect to the variance as

$$R^{\mathbb{V}\mathrm{ar}}_{\tau} = \frac{\mathbb{V}\mathrm{ar}(X(\tau)) - \mathbb{V}\mathrm{ar}_{\bar{p}_{\epsilon_1,\alpha_1}}(X)}{\mathbb{V}\mathrm{ar}(X(\tau)) - \mathbb{V}\mathrm{ar}_{\bar{p}_{\epsilon_0,\alpha_0}}(X)}, \tag{3.6}$$

where $\mathbb{V}\mathrm{ar}_{\bar{p}_{\epsilon,\alpha}}(X)$ simply denotes the variance of the probability distribution defined by $\bar{p}_{\epsilon,\alpha}$ and $\mathbb{V}\mathrm{ar}(X(\tau))$ is the variance of the process (3.1) at time τ. Note that, with respect to Eq. (3.1), the signs of the numerator and denominator of Eq. (3.6) where reversed, which has no effect except for emphasizing that both are positive quantities. The example in Sec. IV illustrates the correspondence between R_τ and $R^{\mathbb{V}\mathrm{ar}}_{\tau}$.

Another quantity used to measure resilience is that of the characteristic return time to equilibrium after perturbation [see Refs. 8,10,21]. In the context of our formulation, this concept is related to the rate at which $\mathbb{E}S(X(t))$ diverges from $\bar{S}_{\epsilon_0,\alpha_0}$ towards $\bar{S}_{\epsilon_1,\alpha_0}$ right after the environmental perturbation, and the rate at which $\mathbb{E}S(X(t))$ converges to $\bar{S}_{\epsilon_1,\alpha_1}$ after the adaptation. These rates are encoded in the largest nonzero eigenvalue $\rho_{\epsilon,\alpha}$ of the forward operator $\mathcal{L}^*_{\epsilon,\alpha}$ in Eq. (2.2) at the different stages of the process. The proposed resilience measure R_τ can be viewed as a comparison between the values of the inverse timescale $\rho_{\epsilon_1,\alpha_0}$, λ and $\rho_{\epsilon_1,\alpha_1}$. A resilient system would be one in which $|\rho_{\epsilon_1,\alpha_1}|$ is large compared to $|\rho_{\epsilon_1,\alpha_0}|$.

D. Estimating ecological resilience

Linear response theory can be used to estimate the effect that a perturbation has on the distribution and averages of a nonlinear stochastic process. Namely, assuming both $\Delta\epsilon := \epsilon_1 - \epsilon_0$ and $\Delta\alpha := \alpha_1 - \alpha_0$ are small, we will use linear response theory to give estimates to $\bar{S}_{\epsilon_1,\alpha_1} - \bar{S}_{\epsilon_0,\alpha_0}$ and $\bar{S}^{\tau}_{\epsilon_1,\alpha_0} - \bar{S}_{\epsilon_0,\alpha_0}$ which can, in turn, be used to give approximations to R_τ in Eq. (3.1).

For definiteness, consider the process X_{ϵ_1,α_0} with initial distribution $X_{\epsilon_1,\alpha_0}(0) \sim \bar{p}_{\epsilon_0,\alpha_0}$. By choosing different values for ϵ in the dynamics for $t > 0$ and the initial distribution, we are modeling a system that experiences a press disturbance $\epsilon_0 \to \epsilon_1$ for all $t > 0$ (see Fig. 1). Since we are assuming that F_{ϵ_0,α_0} in Eq. (2.1) is differentiable with respect to ϵ, the disturbance produces a perturbation on the drift, which to first order on $\Delta\epsilon$ is

$$F_{\epsilon_0,\alpha_0} \to F_{\epsilon_0,\alpha_0} + \mathbf{J}_\epsilon F_{\epsilon_0,\alpha_0} \Delta\epsilon, \tag{3.7}$$

where $\mathbf{J}_\epsilon F_{\epsilon_0,\alpha_0}$ denotes the Jacobian of the vector field F_{ϵ_0,α_0} with respect to the vector parameter $\epsilon \in \mathbb{R}^P$. Linear response provides an approximate expression for the probability density of the disturbed process and averages of any observable, in terms of the un-disturbed distribution $\bar{p}_{\epsilon_0,\alpha_0}$. Note that the corresponding perturbation on the Fokker-Planck operator is

$$\begin{aligned}\mathcal{L}^*_{\epsilon_0,\alpha_0}[p] &\to \mathcal{L}^*_{\epsilon_0,\alpha_0}[p] - \nabla\cdot(p\,\mathbf{J}_\epsilon F_{\epsilon_0,\alpha_0}\,\Delta\epsilon)\\ &= \mathcal{L}^*_{\epsilon_0,\alpha_0}[p] + \Delta\epsilon\cdot\ell_\epsilon[p],\end{aligned} \tag{3.8}$$

where the operator ℓ_ϵ is defined coordinate-wise as follows:

$$\ell_\epsilon[p]^{(i)} = -\sum_{j=1}^{N} \frac{\partial}{\partial x^{(j)}}\left(p\frac{\partial F^{(j)}_{\epsilon_0,\alpha_0}}{\partial\epsilon^{(i)}}\right), \qquad i = 1,\dots,P. \tag{3.9}$$

If we approximate to first order the expectation of S under the perturbation as

$$\mathbb{E}_{\bar{p}_{\epsilon_0,\alpha_0}}(S(X_{\epsilon_1,\alpha_0}(t))) \approx \bar{S}_{\epsilon_0,\alpha_0} + \Delta\epsilon\cdot\Delta_\epsilon\bar{S}_{\epsilon_0,\alpha_0}(t), \tag{3.10}$$

then linear response theory says that the correction $\Delta_\epsilon\bar{S}_{\epsilon_0,\alpha_0}(t)$ can be written in terms of the forward evolution operator as

$$\Delta_\epsilon\bar{S}_{\epsilon_0,\alpha_0}(t) = \int_0^t\int e^{s\mathcal{L}^*_{\alpha_0,\epsilon_0}}[\ell_\epsilon[\bar{p}_{\epsilon_0,\alpha_0}]](x)\,S(x)\,dx\,ds. \tag{3.11}$$

See Ref. [22] for details.

Note that Eq. (3.11) is written in terms exclusively of the un-perturbed dynamics and, by Eq. (2.7), can be expanded out as a correlation over paths of the process X_{ϵ_0,α_0},

$$\Delta_\epsilon\bar{S}_{\epsilon_0,\alpha_0}(t) = \int_0^t \mathbb{E}_{\bar{p}_{\epsilon_0,\alpha_0}}\{r_\epsilon[\bar{p}_{\epsilon_0,\alpha_0}](X_{\epsilon_0,\alpha_0}(0))S(X_{\epsilon_0,\alpha_0}(s))\}\,ds, \tag{3.12}$$

where r_ϵ denotes the operator

$$r_\epsilon[p] = \frac{\ell_\epsilon[p]}{p} \tag{3.13}$$

for suitable $p : \mathbb{R}^N \to \mathbb{R}$.

The approximation (3.10) at $t = \tau$ provides an estimate for

$$\bar{S}^\tau_{\epsilon_1,\alpha_0} \approx \bar{S}_{\epsilon_0,\alpha_0} + \Delta\epsilon\cdot\Delta_\epsilon\bar{S}^\tau_{\epsilon_0,\alpha_0}. \tag{3.14}$$

To estimate the perturbation $\Delta_\epsilon\bar{S}^\tau_{\epsilon_0,\alpha_0}$ we can multiply (3.10) times $\lambda e^{-\lambda t}$ and integrate with respect to t. We obtain

$$\begin{aligned}\Delta_\epsilon\bar{S}^\tau_{\epsilon_0,\alpha_0} &= \iint_0^\infty e^{-\lambda s}e^{s\mathcal{L}_{\alpha_0,\epsilon_0}}[S](x)\,ds\,\ell_\epsilon[\bar{p}_{\epsilon_0,\alpha_0}](x)\,dx\\ &= \int \mathcal{R}^{(\lambda)}_{\epsilon_0,\alpha_0}[S](x)\ell_\epsilon[\bar{p}_{\epsilon_0,\alpha_0}](x)\,dx.\end{aligned} \tag{3.15}$$

As previously mentioned, the estimate (3.15) is useful whenever the resolvent can be computed analytically or numerically. In general, we can also take expectations of Eq. (3.12) with respect to τ to obtain an estimate of $\bar{S}^\tau_{\epsilon_1,\alpha_0}$ as a correlation suitable for simulations,

$$\Delta_\epsilon\bar{S}^\tau_{\epsilon_0,\alpha_0} = \mathbb{E}_{\bar{p}_{\epsilon_0,\alpha_0}}\{r_\epsilon[\bar{p}_{\epsilon_0,\alpha_0}](X_{\epsilon_0,\alpha_0}(0))S(X_{\epsilon_0,\alpha_0}(\tau))\}. \tag{3.16}$$

Replacing the terms $\bar{S}^\tau_{\epsilon_1,\alpha_0}$ in the expression of Eq. (3.1) by its approximation in Eq. (3.14) we obtain the following more practical expression for the resilience,

$$R_\tau \approx \tilde{R}_\tau = 1 - \frac{\bar{S}_{\epsilon_0,\alpha_0} - \bar{S}_{\epsilon_1,\alpha_1}}{-\Delta\epsilon\cdot\Delta_\epsilon\bar{S}^\tau_{\epsilon_0,\alpha_0}}. \tag{3.17}$$

Note that the numerator in Eq. (3.17) contains the extremes values in Eq. (3.2), namely the "before and after" of a population that has gone through the invariance-perturbation-adaptation sequence. The denominator is positive for stressful environmental perturbations and models the average "damage" caused by the perturbation. It provides an alternative to calculating the challenging term $\bar{S}^\tau_{\epsilon_1,\alpha_0}$ in Eq. (3.1). The term that is subtracted from one is therefore the total long-term change in average success as a fraction of the total damage.

A further estimate for the numerator $\bar{S}_{\epsilon_1,\alpha_1} - \bar{S}_{\epsilon_0,\alpha_0}$ in Eq. (3.17) may be obtained for small $\Delta\epsilon$, $\Delta\alpha$ by straightforward differentiation. Assuming smoothness of the invariant distribution and of S with respect to ϵ and α, we can write to first order

$$\bar{S}_{\epsilon_1,\alpha_1} - \bar{S}_{\epsilon_0,\alpha_0} \approx \Delta\epsilon\cdot\nabla_\epsilon\bar{S}_{\epsilon_0,\alpha_0} + \Delta\alpha\cdot\nabla_\alpha\bar{S}_{\epsilon_0,\alpha_0}, \tag{3.18}$$

where ∇_ϵ and ∇_α denote, respectively, the gradients with respect to the parameters ϵ and α of the invariant expectation of the success at $\alpha = \alpha_0, \epsilon = \epsilon_0$. Equation (3.18) approximates the numerator in Eq. (3.17) as a combination of the sensitivities of the system to the different parameters and yields yet another approximate expression for the resilience

$$R_\tau \approx \hat{R}_\tau = 1 - \frac{\Delta\epsilon\cdot\nabla_\epsilon\bar{S}_{\epsilon_0,\alpha_0}}{\Delta\epsilon\cdot\Delta_\epsilon\bar{S}^\tau_{\epsilon_0,\alpha_0}} - \frac{\Delta\alpha\cdot\nabla_\alpha\bar{S}_{\epsilon_0,\alpha_0}}{\Delta\epsilon\cdot\Delta_\epsilon\bar{S}^\tau_{\epsilon_0,\alpha_0}}. \tag{3.19}$$

For the sake of argument, suppose the environmental parameter is one-dimensional ($P = 1$) in Eq. (3.19), then

$$\hat{R}_\tau = 1 - \frac{\nabla_\epsilon\bar{S}_{\epsilon_0,\alpha_0}}{\Delta_\epsilon\bar{S}^\tau_{\epsilon_0,\alpha_0}} + \frac{\nabla_\alpha\bar{S}_{\epsilon_0,\alpha_0}}{-\Delta_\epsilon\bar{S}^\tau_{\epsilon_0,\alpha_0}}\cdot\frac{\Delta\alpha}{\Delta\epsilon} \tag{3.20}$$

$$=: 1 - R^{\mathrm{Env}}_\tau + R^{\mathrm{Ad}}_\tau\cdot\frac{\Delta\alpha}{\Delta\epsilon}. \tag{3.21}$$

The approximation $\hat{R}_\tau$ to R^τ separates the proposed resilience measured into its competing terms. The term R^{Env}_τ is positive and depends only on the initial state, the effect of the environmental disturbance, and how much time the system takes to react. It rescales the sensitivity of the system to changes in ϵ with respect to the total damage. The term $R^{\mathrm{Ad}}_\tau\cdot\frac{\Delta\alpha}{\Delta\epsilon}$ is positive for resilient systems. Its factor $\Delta\alpha/\Delta\epsilon \approx \frac{d\alpha}{d\epsilon}(\epsilon_0)$ represents the adaptation strategy (recall the discussion after Eq. (3.1) around the underlying unresolved adaptation dynamics) and R^{Ad}_τ models the effect of the adaptation as compared to the damage incurred by the environmental perturbation.

Computing the gradients with respect to α and ϵ in expressions (3.19) or (3.20) requires evaluation or measurement of the dynamics under the invariant distribution of a perturbed system along each of the P and Q components of the parameters. For an alternate expression we can use the following result that, as in the linear response theory derivations, allows for computation of derivatives in terms only of expected values of a particular observable of the un-perturbed system.

Proposition III.2. If S is independent of ϵ, then

$$\begin{aligned}\nabla_\epsilon \bar{S}_{\epsilon_0,\alpha_0} &= \int S(x)\nabla_\epsilon \bar{p}_{\epsilon_0,\alpha_0}(x)\,dx\\ &= \mathbb{E}_{\bar{p}_{\epsilon_0,\alpha_0}}(\mathbf{J}_\epsilon F_{\epsilon_0,\alpha_0}\nabla\psi_S),\end{aligned}\tag{3.22}$$

where ψ_S is the solution to Poisson equation $-\mathcal{L}_{\epsilon_0,\alpha_0}[\psi_S] = S$. Similarly for $\nabla_\alpha \bar{S}_{\epsilon_0,\alpha_0}$.

Proof. By the definition of ψ_S we can write

$$\begin{aligned}\nabla_\epsilon \bar{S}_{\epsilon_0,\alpha_0} &= -\int \mathcal{L}_{\epsilon_0,\alpha_0}[\psi_S]\nabla_\epsilon \bar{p}_{\epsilon_0,\alpha_0}(x)\,dx\\ &= -\int \psi_S(x)\mathcal{L}^*_{\alpha_0,\epsilon_0}[\nabla_\epsilon \bar{p}_{\epsilon_0,\alpha_0}](x)\,dx.\end{aligned}$$

Using the particular form of the forward operator (2.5) and the fact that $\mathcal{L}^*_{\epsilon_0,\alpha_0}[\bar{p}_{\epsilon_0,\alpha_0}] = 0$, one can write

$$\mathcal{L}^*_{\alpha_0,\epsilon_0}[\nabla_\epsilon \bar{p}_{\epsilon_0,\alpha_0}] = \nabla(\bar{p}_{\epsilon_0,\alpha_0}\mathbf{J}_\epsilon F_{\epsilon_0,\alpha_0}).$$

Finally, integration by parts yields

$$\nabla_\epsilon \bar{S}_{\epsilon_0,\alpha_0} = \int \nabla\psi_S(x)\bar{p}_{\epsilon_0,\alpha_0}(x)\mathbf{J}_\epsilon F_{\epsilon_0,\alpha_0}(x)\,dx$$

as desired. ∎

Note that a slightly more convoluted proof of Proposition III.2 can be obtained using the linear response representation (3.11), the identity $\int_0^t e^{s\mathcal{L}_{\alpha_0,\epsilon_0}}\,ds = (I - e^{t\mathcal{L}_{\alpha_0,\epsilon_0}})[(-\mathcal{L}_{\alpha_0,\epsilon_0})^{-1}]$, and passing to the limit as $t \to \infty$. See Pavliotis [22, Sec. 9.3]. A closely related formula for the sensitivity of a finite-state Markov chains to general perturbations has been presented in Ref. [30].

IV. EXAMPLE: A GRADIENT-DRIVEN STOCHASTIC DIFFERENTIAL EQUATION

We illustrate the measure of resilience through adaptation in a case where the invariant distribution generated by Eq. (2.1) can be computed analytically. We consider a gradient-driven Langevin equation with a one-dimensional quartic potential (also known as Smoluchowski diffusion equation),

$$dX = -\frac{\partial V_{\epsilon,\alpha}}{\partial x}(X)dt + \sigma\,dW_t, \quad t > 0, \tag{4.1}$$

$$V_{\epsilon,\alpha}(x) = \alpha^{(1)}x^4 - \alpha^{(2)}x^3 + \epsilon x - c, \quad x \in \mathbb{R}. \tag{4.2}$$

The constant c ensures that $V_{\epsilon,\alpha}(x) \geqslant 0$ for all $x \in \mathbb{R}$. The adaptation parameter is two-dimensional $\alpha = (\alpha^{(1)}, \alpha^{(2)}) \in [0.5, 1] \times [1, 2]$. The environmental parameter takes values in $\epsilon \in [0, 2]$. Namely, $P = 1$ and $Q = 2$, which exemplifies the typical case where regulatory parameters are more numerous than environmental parameters.

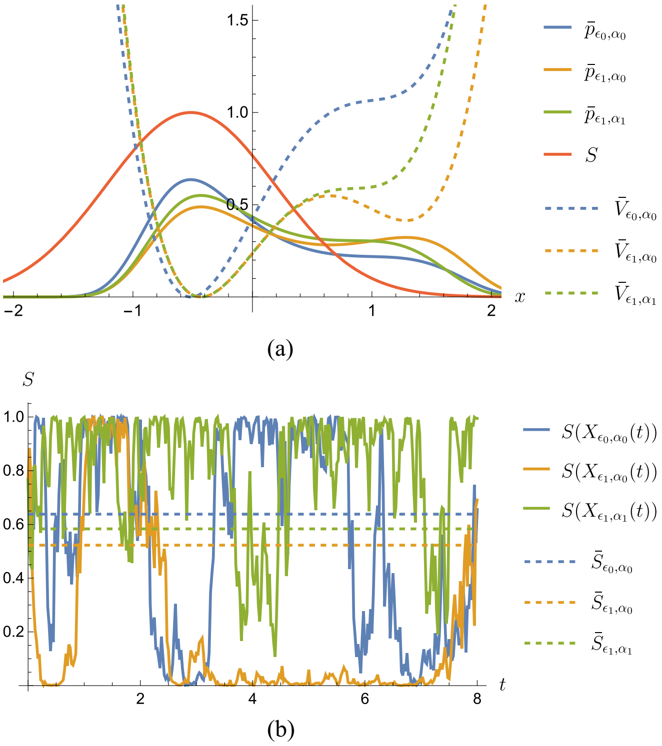

FIG. 2. (a) Stationary distributions $\bar{p}_{\epsilon,\alpha}$ and potentials $V_{\epsilon,\alpha}$ for an invariance-perturbation-adaptation sequence with $\sigma^2 = 2$, $\epsilon_0 = 1.2$ $\epsilon_1 = 0.8$, $\alpha_0 = (0.56, 1.12)$ and $\alpha_1 = (0.63, 1.07)$. Note the unimodality for (ϵ_0, α_0) and (ϵ_1, α_0), and bimodality for (ϵ_1, α_1). The success function S is shown in red for comparison. (b) Paths of $S(X_{\epsilon,\alpha}(t))$ for one realization of the process (4.1) in each of the parameters combinations in panel (a). Dashed horizontal lines show the mean of S with respect to the corresponding invariant distribution. Note that the process spends much more time in low success states for the bimodal configuration.

For any combination (ϵ, α) in those ranges, the potential $V_{\epsilon,\alpha}$ is confining and therefore the solution process $X_{\epsilon,\alpha}$ to Eq. (4.1) is ergodic with a unique invariant distribution density given by

$$\bar{p}_{\epsilon,\alpha}(x) = \frac{1}{Z_{\epsilon,\alpha}}\exp\left(-\frac{2}{\sigma^2}V_{\epsilon,\alpha}(x)\right), \quad x \in \mathbb{R}, \tag{4.3}$$

where $Z_{\epsilon,\alpha}$ is a constant ensuring that $\bar{p}_{\epsilon,\alpha}$ integrates to unity. The equilibrium states of the potential $V_{\epsilon,\alpha}$ correspond to the roots of $\frac{\partial}{\partial x}V_{\epsilon,\alpha}$ and to the local maxima of $\bar{p}_{\epsilon,\alpha}$. In fact, the system undergoes a "supercritical pitchfork" bifurcation at

$$\epsilon_b(\alpha) = \frac{(\alpha^{(2)})^3}{2(\alpha^{(1)})^2}, \tag{4.4}$$

having one stable equilibrium if $\epsilon > \epsilon_b$ and two if $\epsilon < \epsilon_b$ [31]. See Fig. 2(a).

The disturbances to ϵ and α in system (4.1) are performed according to a specific protocol of invariance-perturbation-adaptation we now explain. Suppose that "normal" operating conditions encoded in ϵ_0, α_0 satisfy $\epsilon_0 > \epsilon_b(\alpha_0)$ so that there is only one equilibrium solution which, for the range of parameters considered here, is near $x = -1/2$ [see Fig. 2(a)]. We will consider this as the preferred/most successful state of the system. The environmental perturbation $\epsilon_0 \to \epsilon_1$ is such that $\epsilon_1 < \epsilon_b(\alpha_0)$, inducing a pitchfork bifurcation that creates a second stable equilibrium in the positive real line.

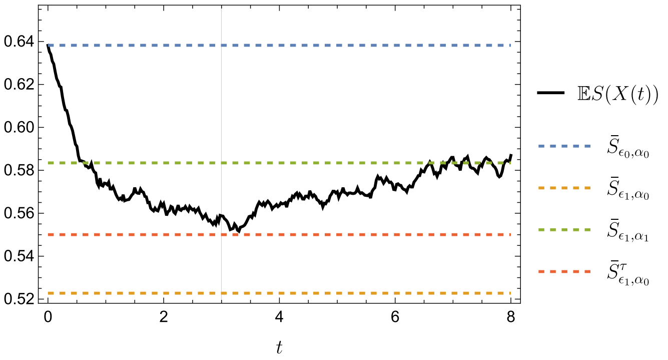

FIG. 3. Ensemble mean $\mathbb{E}S(X(t))$ for X given by Eq. (3.1) with $\sigma, \epsilon_0, \epsilon_1, \alpha_0, \alpha_1$ as in Fig. 2, and $\lambda = 1/3$. The mean was computed from a sample of 6000 paths. Horizontal dashed lines mark the invariant means of S under each scenario and the mean of $S(X(\tau))$. The vertical line marks $t = \mathbb{E}(\tau) = 1/\lambda$ The resilience is $R = 0.44$. The value $\bar{S}_{\epsilon_1,\alpha_0}$ is the long-term mean of the success in the do-nothing scenario, and plays no role in the computation of the resilience.

Paths of X_{ϵ_1,α_0} will then likely spend time in the basin of attraction of this second stable equilibrium, which we will presume is highly undesirable. The preference of $x = -1/2$ over the second equilibrium is is encoded for this example in the success function by defining

$$S(x) = e^{-(x+1/2)^2}, \quad x \in \mathbb{R}. \tag{4.5}$$

The value of $S(X(t))$ gives therefore an idea of how close the system is to "preferred" operating conditions.

The adaptation $\alpha_0 \to \alpha_1$ takes place instantly at a random reaction time $\tau \sim \exp(\lambda)$ after the environmental perturbation. We consider the following adaptation strategy: $\Delta\alpha$ is a vector in the direction of $\nabla_\alpha \bar{S}_{\epsilon_1,\alpha_0}$ such that for $\alpha_1 = \alpha_0 + \Delta\alpha$, $\epsilon_b(\alpha_1) < \epsilon_1$ holds. The resulting adaptation is, by construction, such that the system reverts to the case $\epsilon_1 > \epsilon_b(\alpha_1)$ where only the preferred stable equilibrium remains and $\bar{p}_{\epsilon_1,\alpha_1}$ is again unimodal.

The choice of S in Eq. (4.5) and adaptation strategy ensures that the prescribed environmental and adaptation perturbations are, respectively, stressful and beneficial in average. Namely, in the notation of Eq. (2.8)

$$\bar{S}_{\epsilon_0,\alpha_0} > \bar{S}_{\epsilon_1,\alpha_0}, \quad \bar{S}_{\epsilon_1,\alpha_1} > \bar{S}_{\epsilon_1,\alpha_0}. \tag{4.6}$$

This strategy models the case in which the system can correct the bifurcation while at the same time ensuring a future mean success better than the do-nothing scenario $\bar{S}_{\epsilon_1,\alpha_0}$.

Figure 2(a) depicts the potentials and stationary distributions in one example of the whole invariance-perturbation-adaptation sequence. Superimposed is the success function S. Figure 2(b) shows the success function $S(X_{\epsilon,\alpha}(t))$ along a single path for each regime. It highlights the noisy nature of the dynamics, including the episodic switches between basins of attraction in each of the three operating regimes, namely realizations exhibiting what in Sec. III A we referred to as "path-wise resilience." The expectations of the success function with respect to each of the stationary distributions are depicted as well.

Figure 3 depicts the time evolution of the ensemble mean $\mathbb{E}S(X(t))$ for the process constructed as in Eq. (3.1) with the dynamics of Eq. (4.1), for a single combination of the invariance-perturbation-adaptation protocol $\epsilon_0, \epsilon_1, \alpha_0, \alpha_1$ described above. All the terms in the usual definitions of resilience, including R given in Eq. (3.3), can be "read-off" from this figure. See for example the discussions around Fig. 4(d) in Ref. [6] and Fig. 5 in Ref. [5]. Note that $\mathbb{E}S(X(t))$ in Fig. 3 above varies between the initial and final values given by Eq. (3.2) and that its minimum $\min_{t\geqslant 0} \mathbb{E}(S(X(t))$ is close to the value of $\bar{S}^{\tau}_{\epsilon_1,\alpha_0}$.

To robustly test our proposal R_τ in Eq. (III.1) as a coherent measure of adaptation resilience, we conducted numerical experiments on different configurations of Eq. (4.1). We considered 64 different populations, each with a different value of α_0. All populations undergo the same environmental bifurcation-inducing disturbance $\epsilon_0 = 0.8 \to \epsilon_1 = 1.2$. The adaptation strategy followed by the populations is as described above, and results in different a value of α_1 for each example. Figure 4 shows the location of α_0 and α_1 for each system with respect to bifurcation thresholds.

The numerical results are depicted in Fig. 5. The dashed line indicates a perfect match between R and R_τ. We note that the data is increasing, from which we conclude that R_τ

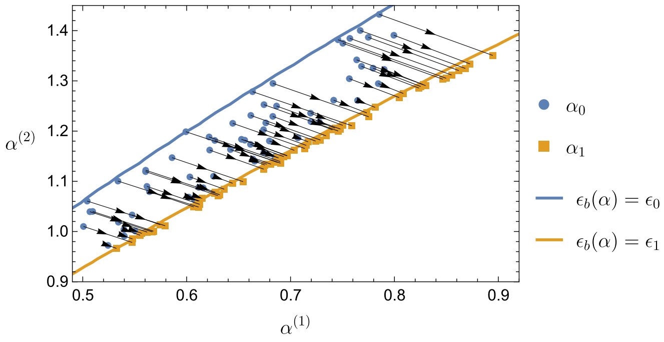

FIG. 4. Values of α_0, α_1 used in the examples for numerically computation of R and R_τ. The solid lines are contour lines for the bifurcation threshold ϵ_b in Eq. (4.4) for ϵ_0 and ϵ_1 as in Fig. 2. Black arrows show that each adaption follows the strategy leading to Eq. (4.6): from $\epsilon_b(\alpha_0) > \epsilon_1$ and hence having two stable equilibria, to $\epsilon_b(\alpha_1) < \epsilon_1$ and a single stable equilibrium after adapting.

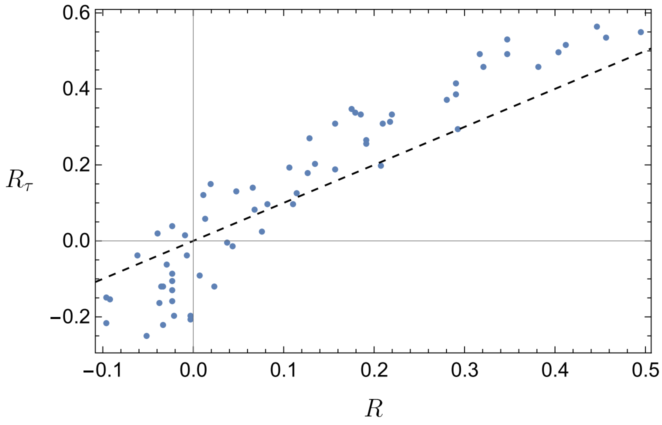

FIG. 5. Comparison between R and R_τ for the 64 combination of parameters shown in Fig. 4. The dashed line marks equality.

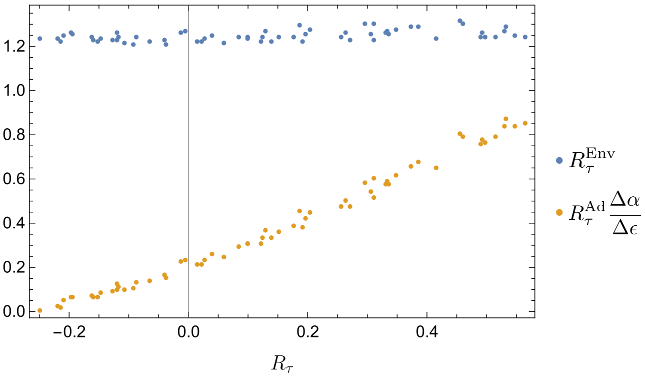

FIG. 6. Comparison between the environmental and adaptation components of R_τ in Eq. (III.1). In this example, most of the variability in the resilience comes from the adaptation term.

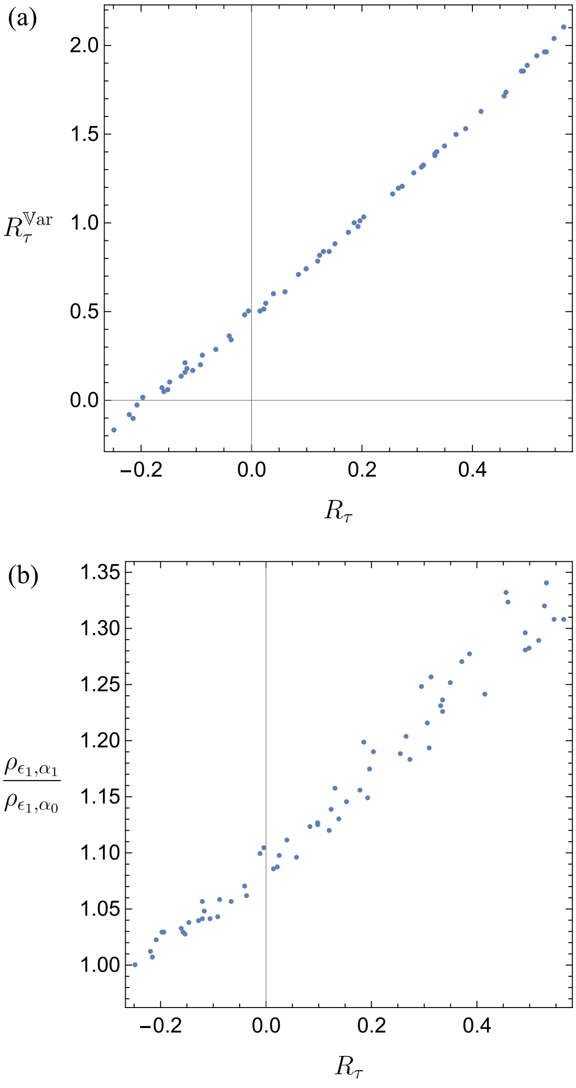

FIG. 8. (a) Comparison between R_τ and the measure of resilience $R_\tau^{\mathbb{V}\mathrm{ar}}$ in Eq. (3.6) based on the variance of $X_{\epsilon,\alpha}$. (b) Comparison between R_τ and the ratio between the dominant eigenvalues of the adapted vs nonadapted system.

can be used to establish when one system is more resilient than other in the usual sense. Note also that the two measures tend to agree for the most resilient examples, which in this case simply transpires the good approximation of $\bar{S}^{\tau}_{\epsilon_1,\alpha_0}$ to $\min \mathbb{E}S(X(t))$. Those examples for which $R_\tau < 0$ correspond to cases in which $\bar{S}_{\epsilon_1,\alpha_1} < \bar{S}^{\tau}_{\epsilon_1,\alpha_0}$, namely the adaptation $\alpha_0 \to \alpha_1$ did not increase the mean success as compared with the mean success at τ.

Figure 6 shows the approximate components of R_τ as per equation (3.21). The environmental component is essentially constant throughout our examples, and most of the variation of the resilience is due to the adaptation component.

In Sec. III C we derived more practical measures to estimate R or R_τ, that we foresee as practical since they can be informed by field data. In Fig. 7 we evaluate how $\tilde{R}_\tau$ in Eq. (3.17) and $\hat{R}_\tau$ in Eq. (3.19) compare to the estimate R_τ. We used the same ensemble and parameter values. The figures suggest that the empirical versions of these are good approximations for the resilience of the system.

As mentioned in Sec. III C, R_τ can be compared to existing measures or resilience for noisy systems. The value $R_\tau^{\mathbb{V}\mathrm{ar}}$ in Eq. (3.6) aims at quantifying resilience by analyzing the changes to the variance in X [21]. Namely, we make $S(x) = S_{\epsilon,\alpha}(x) = (x - \bar{x}_{\epsilon,\alpha})^2$ where $\bar{x}_{\epsilon,\alpha}$ is the mean of the distribution $\bar{p}_{\epsilon,\alpha}$. Figure 8(a) shows a comparison between R_τ and $R_\tau^{\mathbb{V}\mathrm{ar}}$ for all the examples. Again, since the pattern is increasing, the resilience R_τ can be used as a proxy for a resilience measure built on the variability induced by the disturbances. This is simply the result of choosing a success function S in Eq. (4.5) that is maximized near the mean $\bar{x}_{\epsilon_0,\alpha_0}$.

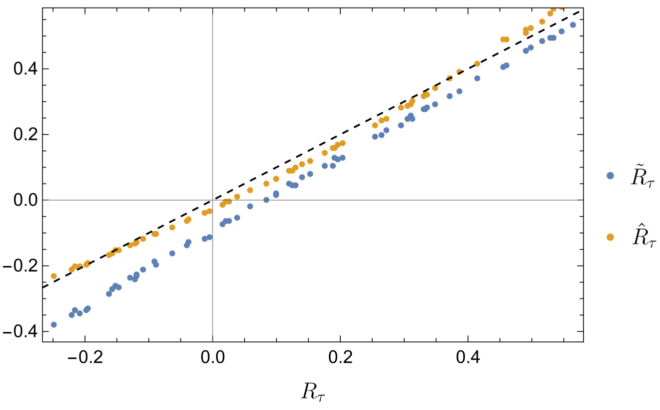

FIG. 7. Comparison between R_τ and its approximations $\tilde{R}_\tau$ [Eq. (3.17)][and $\hat{R}_\tau$ [Eq. (3.19)] obtained through linear response theory. The dashed line marks equality.

For the model in Eq. (4.1), one can numerically compute the largest eigenvalues $\rho_{\epsilon,\alpha}$ of the forward operator $\mathcal{L}^*_{\epsilon,\alpha}$ in Eq. (2.5) for any ϵ, α. Thus we can assess whether R_τ gives any information about the rates of exit and return to the equilibrium after the perturbation. Note that a resilient system would be one in which the eigenvalue after adaptation $|\rho_{\epsilon_1,\alpha_1}|$ is large compared to the eigenvalue after the environmental perturbation $|\rho_{\epsilon_1,\alpha_0}|$. Figure 8(b) shows a comparison between R_τ and the ratio $|\rho_{\epsilon_1,\alpha_1}|/|\rho_{\epsilon_1,\alpha_0}|$ for each example, indicating that R_τ is consistent with this interpretation of resilience.

In summary, the functional R_τ provides a measure of resilience that, at least for the adaptation strategy used in the examples shown here, is coherent with various notions of resilience used in the context of noisy dynamical systems.

V. DISCUSSION AND CONCLUSIONS

We have proposed a measure of ecological resilience which quantifies the success of a forced/dissipative system to adapt following an initial applied stress. The relevance of our resilience measure to biological systems, rests upon the assumption that the time evolution of the biological system is described by a stochastic differential equation with a initial stationary probability distribution (prior to the application of a stress). The stochastic nature of the process means that for each starting value of the system there is an ensemble of possible histories (paths). Moreover, our conceptual model also accounts for the random variability among states or subsystems within an organism.

At the mechanistic level, our measure of resilience is strongly inspired by the homeodynamic nature of biological systems that react to some type of imposed stress with an eventual physiological adaptation. Unlike most measures of resilience, we are suggesting that the time history of a well-chosen success observable is essential to the determination of the organism's resilience to adaptation. Further, we argue that the resilience can be best captured in the ensemble mean among a population of individual subsystems which can have different starting conditions, and random responses to stress. We are suggesting here that a typical success history in noisy/forced systems, as typified by Fig. 3, can only be uncovered by ensemble methods such as those proposed in this study.

It follows from the approximation for R_τ in Eq. (3.17) that low resilience will occur in systems with low values of $|\Delta_\epsilon \bar{S}^\tau_{\epsilon_0,t_0}|$, which in Eq. (3.16) is written as a temporal correlation between functionals of the process X. The relationship between correlations and critical transitions in complex systems is now well-established as in the concept of "critical slowing down" of correlations [18,19,21]. Indeed, the quantity $\Delta_\epsilon \bar{S}^\tau_{\epsilon_0,t_0}$ in the example of Sec. IV is related to how often system paths transition towards the second stable equilibrium. Resilience, however, must also consider the ability of the system to recover. Our characterization (3.21) of R^{Env}_τ and R^{Ad}_τ provides the appropriate quantities with respect to which $\Delta_\epsilon \bar{S}^\tau_{\epsilon_0,t_0}$ must be compared in order obtain a more complete picture.

We now address the practicality of our definition of resilience to adaptation as a proposed measure of resilience. We do so by showing how it may be estimated using actual experimental, field, or simulation data.

First of all, a dynamic model is not intrinsic to the definition of the resilience measures R or R_τ, and it is *not* required to estimate resilience from data. Knowing the densities $\bar{p}_{\epsilon,\alpha}$ over the state space is also not a requirement. The estimation of R_τ requires only *samples* from such densities. Namely, to identify, simulate, or prepare an ensemble of individual systems that have been operating under constant environmental conditions, subject them to an environmental disturbance, and measuring the chosen success function S through the adaptation process. The ensemble must be numerous enough to accurately compute expected values of S from sample averages. For estimating R, the values of $S(X(t))$ must be sampled from the field sufficiently regularly in time to capture (as in Fig. 3) the initial, minimum, and limiting values of $\mathbb{E}S(X(t))$ required by the definition (3.3). Our proposal R_τ, however, requires the detection of the moment at which adaptation occurs in each individual. Measuring success at such moment is the equivalent of sampling the random variable $S(X(\tau))$. In this case only three data points are required from each system: the unperturbed state, the moment of adaptation, and a final state when the population is observed to revert to its new statistical equilibrium.

Linear response theory yields further tools to estimate R_τ, as detailed in Sec. III D. These estimates take the form of expectations and correlations of specific functionals of the process X. See Eqs. (3.5), (3.12), and (3.16) and Proposition III.2. This estimates can be performed by a combination of experimental data assimilation, simulation and analytical tools, depending on the specific model. A key feature of our framework is that different types of approximation to R_τ can achieved depending on the level of detail of the available mathematical model. In its full form, every component of the resilience in Eq. (3.21) can be estimated by simulating only the unperturbed process X_{ϵ_0,α_0}.

With regards to the definition of resilience in terms of an almost arbitrary success function S, we argue that it yields a more useful and encompassing framework, since notions of stress, well-being, or health can in many case be subjective and application-dependent: S can be any observable of interest that quantifies the degree to which a system is successful. In principle, S does not have to be positive, bounded, or continuous for the definition of R_τ to make sense, however, we suppose that $S \in \mathrm{Dom}(\mathcal{L}_{\epsilon,\alpha})$ in Eq. (2.2), which typically contains only bounded, smooth functions.

This approach is antithetical to the idea that there is a universal notion of resilience even when confronted with the same systems biology or biological mechanism. For our illustrative example, in Eq. (4.5), we simply defined S as a nonnegative function with a mean centered at an equilibrium point labeled as preferred, with a variance that conveyed how narrowly should success be defined. Alternatively one can propose to measure the resilience of an ensemble of organisms with respect to some biomarker, productivity rate with economic value, or a statistical measure as in the definition (3.6) in $R^{\mathbb{V}\mathrm{ar}}_\tau$.

We exemplified our proposal with a very simple model assuming low-dimensional gradient flow dynamics, and forced and adapted the dynamics by simple changes upon the potential. We argue however, that our approach is amiable to biological systems that not only change through time, but have inherent hierarchies of biological organization. For real-life biological systems, assessing resilience will involve a series of interconnected dynamics described by mathematical or data-driven models (e.g., modeling cell to leaf, leaf to plant, etc).

The more complex model might capture the exact relationship between the state variable and the external forcing, or the dynamics of adaptation itself. Our proposal for resilience to adaptation will go through on these more complex systems, so long as assumptions regarding the stationarity of distribution of the state vector dynamics hold.

The idea of using ensembles and a success function as the means to estimate resilience, is very general. It is, however, limited to situations in which samples from the same distribution can be measured, simulated or observed, and some control over the environmental perturbations can be exerted. The estimation of $S(X(\tau))$ in Eq. (3.1) brings the additional challenge of requiring a way to detect or model when a threshold into adaptation has occurred. The particular model (2.1) has some underlying assumptions that limit the scope of this work. For one, the smoothness and regularity conditions on F might not hold, but more significantly the existence of an invariant distribution might be unknown or impossible to assume. The assumption of linear noise is also problematic in those systems where environmental perturbations increase inherent variability. However, although not explicit in this paper, linear response theory can also be applied to perturbations on $\sigma = \sigma_{\epsilon,\alpha}$ [see 22, for example]. The estimation tools provided in Sec. III D impose more specific limitations which might not hold in general. Specifically, linear response theory requires small $\Delta\epsilon$ and $\Delta\alpha$ and the smoothness of $F_{\epsilon,\alpha}$ and $\bar{p}_{\epsilon,\alpha}$ with respect to ϵ and α.

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