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Bridging Robustness and Resilience for Dynamical Systems in Nature ⋆

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Abstract: Biological systems have evolved to maintain properties that are crucial for survival. Robustness and resilience are associated with a system's ability to preserve its functions despite uncertainties, fluctuations and perturbations, both intrinsic and extrinsic. However, due to the multidisciplinary nature of the research topic, numerous competing definitions of these concepts coexist and often lack a rigorous control-theoretic formulation. Here, we consider a family of ODE systems consisting of stochastic perturbations of a nominal deterministic system and we introduce possible formal definitions of resilience of such a family of systems aimed at probabilistically quantifying its ability to preserve a prescribed attractor. We show that our proposed definitions generalise the notion of probabilistic robustness, and we demonstrate their efficacy when applied to widely used models in biology.

Keywords: Systems biology; Robustness analysis; Probabilistic robustness; Uncertainty descriptions.

1. INTRODUCTION AND MOTIVATION

Natural systems are characterised by a remarkable complexity and, at the same time, by an astounding robustness, in spite of huge uncertainties, variability, or environmental fluctuations. Structural analysis (Blanchini and Giordano, 2021; Blanchini et al., 2012) and robustness analysis (Barmish, 1994) aim at guaranteeing that a property is preserved by a whole family of uncertain systems independent of parameter values, or for all parameter values within a specified set, respectively. However, some properties of interest hold neither structurally nor robustly, but with high probability, and in such cases structural/robust approaches just provide a negative qualitative outcome and cannot quantify to which degree the property holds. Also, systems in nature are subject not only to parametric uncertainties, but also to stochastic perturbations, which may yield regime shifts (Scheffer et al., 2012), mostly understood as shifts among basins of attraction (Ashwin et al., 2012). To address these phenomena, multiple concepts of resilience for networks and dynamical systems have been introduced (Liu et al., 2022), but formal definitions are so far lacking in the literature. Resilience indicators (Dakos et al., 2015; Kuehn, 2011) have also been proposed to quantify the ability of a system to withstand perturbations, while maintaining properties of a given attractor. Their design is still relatively at its infancy and different methods have been suggested recently (Liu et al., 2022; Proverbio et al., 2023). However, most indicators rely on simplistic surrogate models and lack rigorous and widely applicable mathematical definitions.

To address these open questions, we introduce formal definitions of resilience aimed at quantifying the probability that the behaviour of a nominal deterministic system with respect to a prescribed attractor is preserved under stochastic perturbations. We further propose a formal resilience indicator in the form of an attraction time. Our definitions of resilience generalise the notion of probabilistic robustness, in the spirit of Tempo et al. (2013), by considering dynamical disturbances on top of parametric uncertainty, and enable a quantitative assessment of the persistence of system properties, beyond qualitative answers offered by robustness analysis.

Finally, we showcase the efficacy of our proposed definitions in applications to models of biological systems: a reaction-diffusion system for plankton dynamics, exhibiting Turing patterns, and a bistable gene regulation model.

1.1 The need for resilience: A biological example

To motivate the need for a notion of resilience that differs from that of robustness, we resort to a well-known biological example. Consider the system

$$\dot{x} = f_G(x) = -x + a\frac{x^h}{1+x^h} + k, \qquad x(0) = x_0, \qquad (1)$$

where $x(t) \in \mathbb{R},\ t \in [0, \infty)$, represents the concentration of a biochemical species. This is a particular case of a gene regulatory network system, where only activating interactions are assumed to be present in the network, and can be obtained by considering Hill-function dynamics in the full network and applying dimension reduction techniques such as degree-weighted dimension reduction (Gao et al., 2016). System (1) can be associated with the *potential* function $V(x)$, a scalar function such that

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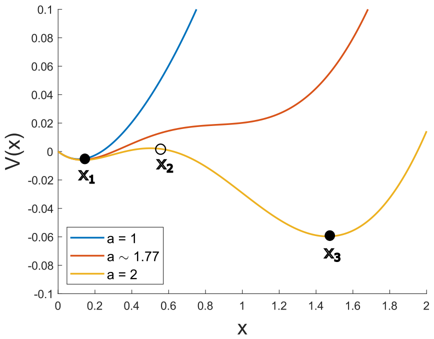

Fig. 1. Potential function $V(x)$ for system (1), with $h = 2$ and $k = 0.1 \in (0, \frac{1}{3\sqrt{3}})$, for different choices of a. The system equilibria (stable, full circle; unstable, empty circle) are shown for the case $a = 2$.

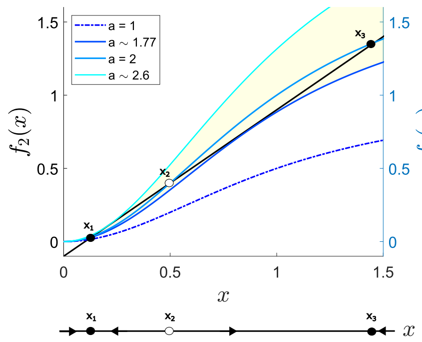

Fig. 2. Top: the intersections of the two functions $f_1(x) = ax^h/(1+x^h)$ and $f_2(x) = x - k$ correspond to setting $f_G(x) = 0$ and identify the equilibria of system (1); we set $h = 2$ and $k = 0.1$, and vary a. At the critical values $a = a_{c,1} \approx 1.77$ and $a = a_{c,2} \approx 2.63$, f_1 is tangent to f_2; the bistable region $a \in (a_{c,1}, a_{c,2})$ is shaded. Bottom: the phase space for system (1), with stable (full circle) and unstable (empty circle) equilibria and vector flows (arrows), for $a = 2$, $h = 2$ and $k = 0.1$.

$f_G(x) = -\nabla V(x)$. The potential is useful to visualise the behaviour of the solutions, in a Lyapunov-like fashion, by studying $V(x(t; x_0))$, i.e., the potential along the solution emanating from $x(0) = x_0$. The potential $V(x)$ for system (1) is shown in Fig. 1 for different choices of a.

Let us consider different combinations of the parameters a, h and k in (1). If $h = 1$, the Hill function reduces to a Michaelis-Menten function, and then the system is *robustly* stable (see Definition 1 in the following). In fact, regardless of how the values of the parameters a and k are chosen in the biologically meaningful range, there is a unique globally asymptotically stable equilibrium:

$$\mathbf{x_1} = \frac{k + a - 1 + \sqrt{(k + a - 1)^2 + 4k}}{2}, \quad \forall a \geq 0,\ k \geq 0\,.$$

As shown by Blanchini et al. (2023), this result is valid for *any* gene regulatory network that exclusively involves Michaelis-Menten interactions, regardless of the parameter values and of the interaction topology. Conversely, if $h \geq 2$, robust stability no longer holds, because the system may be bistable, and admit two locally asymptotically stable equilibria. In fact, when $h \geq 2$ and $k \in (0, \frac{1}{3\sqrt{3}})$, the system may admit three equilibria, of which two ($\mathbf{x_1}$ and $\mathbf{x_3}$) are stable and one ($\mathbf{x_2}$) is unstable. The system equilibria depend on a: there exist $0 < a_{c,1} < a_{c,2}$ such that for $a \in (a_{c,1}, a_{c,2})$ the system is bistable, leading to two contrasting regimes associated with two different stable attractors; see Fig. 2.

Therefore, for $a \in (a_{c,1}, a_{c,2})$ and $k \in (0, \frac{1}{3\sqrt{3}})$ the system does *not* have a unique globally attractive equilibrium when $h \geq 2$. However, although the qualitative *robustness* analysis always yields a negative answer, the behaviour of the system when subject to disturbances changes for different values of $h \geq 2$. As shown in Fig. 3, varying $h \in (2, \infty)$ alters the profile of the potential function associated with the system. In particular, it alters the shape of the basins of attraction around the equilibria, thereby modifying the *resilience* property of the locally asymptotically stable equilibria, understood as the system's ability to reject disturbances while remaining close to equilibrium states, which is necessary for prompt responses to external stimuli and survival of biological systems (Proverbio et al., 2022). A purely qualitative assessment of the robustness of system (1) with respect to the existence of a unique globally asymptotically stable equilibrium does not capture all possible attractor configurations for the system, and a quantitative assessment of the persistence of system properties in the face of disturbances is thus required. To complement robustness, the notion of resilience has been recently introduced in systems biology and network science (Liu et al., 2022). Yet, to date, the numerous definitions of resilience introduced in the literature are mostly heuristic and do not rely on rigorous mathematical formulations.

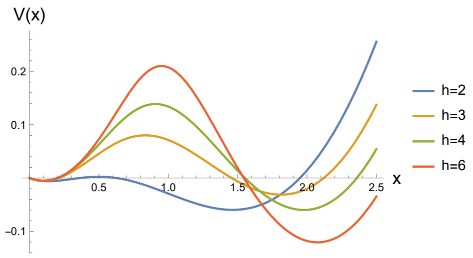

Fig. 3. Potential function $V(x)$ for system (1), with $k = 0.1 \in (0, \frac{1}{3\sqrt{3}})$ and $a = 2 \in (a_{c,1}, a_{c,2})$, for different choices of $h \geq 2$.

In this paper, we propose the first formal definitions of resilience for a class of autonomous ODE systems subject to stochastic noise, and demonstrate their applicability to the analysis of systems in the life sciences.

2. ROBUSTNESS VS. RESILIENCE

2.1 The considered class of systems

We consider a family of systems $\mathcal{F} = \{G_\lambda\}_{\lambda \in \mathcal{I}}$ subject to the following assumptions:

(1) There exists $\lambda_0 \in \mathcal{I}$ such that G_{λ_0} is a *deterministic system* corresponding to an autonomous ODE system

$$\dot{x} = f(x), \quad x(0) = x_0, \quad t \geq 0. \tag{2}$$

Here, $x \in U \subseteq \mathbb{R}^n$, U is open and $f\colon U \to \mathbb{R}^n$ is smooth. The system G_{λ_0} will henceforth be called the *nominal* (deterministic) system.

(2) For $\lambda \in \mathcal{I} \setminus \{\lambda_0\}$, G_λ is obtained from G_{λ_0} via the addition of the *stochastic* stationary noise term η_λ to the right hand side of the ODE in (2). Hence, the state

of G_λ at time $t > 0$ is a random variable, defined on a suitable probability space with probability $\mathbb{P}_\lambda$ that is induced by the stochastic noise η_λ.

Throughout the paper, we assume that the solutions to all the systems in the family $\mathcal{F}$ satisfy existence, uniqueness and extensibility to all times, in the appropriate spaces.

Let A be a closed attractor of G_{λ_0} and $B(A) = \{\chi \in U\colon \lim_{t\to\infty} \operatorname{dist}(x(t;\chi,0),A) = 0\}$ the associated basin of attraction, where $x(t;\chi,0)$ denotes the trajectory of the nominal system G_{λ_0}, with $\eta_{\lambda_0} \equiv 0$, starting from initial condition χ. Given $\lambda \in \mathcal{I} \setminus \{\lambda_0\}$, a natural question to ask is whether the attractor-basin pair $(A, B(A))$ preserves its properties for some/all the systems in $\mathcal{F}$. Before proceeding, we examine two examples from the biological literature.

Example 1. (Turing patterns). The ODE system (13) in (Bashkirtseva et al., 2021), not reported here for brevity, is the finite-difference semi-discretised stochastic ODE version of the following Levin–Segel population equations with diffusion, which are a common model for pattern formation:

$$\begin{aligned} u_t &= au + eu^2 - buv + D_u u_{xx} + \lambda\xi(t,x) \\ v_t &= cuv - dv^2 + D_v v_{xx} + \lambda\eta(t,x) \end{aligned} \tag{3}$$

with zero-flux boundary conditions

$$u_x(0,0) = u_x(0,L) = v_x(0,0) = v_x(0,L) = 0.$$

System (3) is composed of two coupled one-dimensional nonlinear PDEs, where the state variables $u(t,x)$ and $v(t,x)$ represent the density of phytoplankton and herbivore, $x \in [0,L]$, D_u and D_v are the diffusion coefficients, the parameters a, b, c, d and e are positive, λ is the noise intensity, while $\xi(t,x)$ and $\eta(t,x)$ are uncorrelated white Gaussian noise terms. Given initial conditions for the deterministic model (3) with $\lambda = 0$, its solutions exhibit pattern formation (meaning, convergence to periodic wave-like profiles of the graphs of $u(t,\cdot)$ and $v(t,\cdot)$ as $t \to \infty$), provided that the following inequalities hold:

$$\frac{D_u}{D_v} < \left(\sqrt{\frac{b}{d}} - \sqrt{\frac{b}{d} - \frac{e}{c}}\right)^2, \quad bc > ed. \tag{4}$$

For $\lambda > 0$, the stochastic solutions of the system venture away from the deterministic pattern-attractor and fall around it with an appropriate probability distribution.

Here, a family $\mathcal{F}$ is obtained as follows. Assuming that the parameters satisfy (4), let $\mathcal{I} = [0, \lambda_*)$ be an interval of noise intensities that are of interest, and $\lambda_0 = 0$. The systems G_λ, $\lambda \in \mathcal{I}$, correspond to the ODEs obtained from discretising (3) on a sufficiently dense spatial grid. The attractor A is chosen as the pattern generated by G_0, with corresponding basin of attraction $B(A)$.

Example 2. (Gene regulatory network). For the biological example of Section 1.1, the family of systems $\mathcal{F} = \{G_\lambda\}$, where $\lambda \in \mathcal{I} = [0, \lambda_*)$, $\lambda_* > 0$, is such that G_λ, $\lambda \in \mathcal{I}$, is given by the stochastic ODE

$$\dot{x} = f_G(x) + \lambda\eta(t) = -x + a\frac{x^h}{1+x^h} + k + \lambda\eta(t)\,, \tag{5}$$

where $h \geq 2$, $a \in (a_{c,1}, a_{c,2})$ and $\eta(t)$ is an uncorrelated white noise with intensity $\lambda \in \mathcal{I}$. We set $\lambda_0 = 0$, while the attractor A is chosen as a singleton containing one of the two locally stable equilibrium points of G_0, with $B(A)$ being the corresponding basin of attraction.

2.2 Definitions of robustness and resilience

A robust property, and a structural property, for the family of systems $\mathcal{F} = \{G_\lambda\}_{\lambda\in\mathcal{I}}$, as given in Section 2.1, can be defined as follows (Blanchini and Giordano, 2021).

Definition 1. (Robust and structural properties). Given a family of systems $\mathcal{F} = \{G_\lambda\}_{\lambda\in\mathcal{I}}$ and a property $\mathcal{P}$, the property $\mathcal{P}$ is *robustly satisfied* (*robust*) if G_λ enjoys the property $\mathcal{P}$ for every $\lambda \in \mathcal{I}$. If, in addition, the family $\mathcal{F}$ is specified qualitatively by a structure (e.g., a flow graph), without resorting to numerical bounds, the property $\mathcal{P}$ is said to be *structurally satisfied* (*structural*).

Since we are interested in an attractor-basin pair $(A, B(A))$ induced by the nominal deterministic system G_{λ_0}, the property $\mathcal{P}$ is given by

$$\mathcal{P} : (A, B(A)) \text{ is an attractor-basin pair almost surely.} \tag{6}$$

In particular, $\mathcal{P}$ is robust for $\mathcal{F}$ if, for any initial condition $x_0 \in B(A)$ and for all $\lambda \in \mathcal{I} \setminus \{\lambda_0\}$, we have

$$\mathbb{P}_\lambda\left(\left\{\lim_{t\to\infty} \operatorname{dist}(x(t;x_0,\eta_\lambda),A) = 0\right\}\right) = 1, \tag{7}$$

where $x(t;x_0,\eta_\lambda)$ is the solution of system G_λ which emanates from x_0.

As discussed in Section 1, dynamical systems originating in the life-sciences and network theory are often extraordinarily robust with respect to huge uncertainties and environmental fluctuations that induce parameter variations, but do not exhibit an analogous robustness with respect to noise. Their noise rejection property can be captured by the alternative concept of resilience, of which we now aim at proposing rigorous and formal definitions.

Definition 2. (Practical resilience). Consider a family of systems $\mathcal{F} = \{G_\lambda\}_{\lambda\in\mathcal{I}}$ and let $(A, B(A))$ be an attractor-basin pair corresponding to G_{λ_0}. Let the time horizon $\tau \in (0,\infty]$, the distance $\delta \in [0,\infty)$ and the confidence level $\gamma \in (0,1]$ be fixed. Consider the set $A_\varepsilon = \{\chi\colon \operatorname{dist}(\chi,A) \leq \varepsilon\}$, with $0 \leq \varepsilon \leq \delta$. The system G_λ is $(\tau,\gamma,\delta,\varepsilon)$-*practically resilient* if, for all $x_0 \in A_\varepsilon \cap B(A)$,

$$\mathbb{P}_\lambda\left(\sup_{t\in[0,\tau)} \operatorname{dist}(x(t;x_0,\eta_\lambda),A) \leq \delta\right) \geq \gamma.$$

The family $\mathcal{F}$ is $(\tau,\gamma,\delta,\varepsilon)$-*practically resilient* if, for all $x_0 \in A_\varepsilon \cap B(A)$,

$$\inf_{\lambda\in\mathcal{I}\setminus\{\lambda_0\}} \mathbb{P}_\lambda\left(\sup_{t\in[0,\tau)} \operatorname{dist}(x(t;x_0,\eta_\lambda),A) \leq \delta\right) \geq \gamma.$$

Intuitively, the system G_λ, $\lambda \in \mathcal{I} \setminus \{\lambda_0\}$, is $(\tau,\gamma,\delta,\varepsilon)$-practically resilient if, subject to the stochastic noise η_λ, the trajectory $x(t;x_0,\eta_\lambda)$, emanating from an arbitrary point x_0 that lies within an ε-distance from the attractor A, and within its basin of attraction $B(A)$, remains within a δ-distance from A with probability at least γ over the interval $t \in [0,\tau)$. The noise η_λ in the perturbed system may prevent the state from converging to the set A, but at least the nominal dynamics of the system keeps the state close to the attractor A of the nominal system.

The family $\mathcal{F}$ is $(\infty,1,\delta,\delta)$-resilient if, for all $x_0 \in A_\delta \cap B(A)$,

$$\inf_{\lambda\in\mathcal{I}\setminus\{\lambda_0\}} \mathbb{P}_\lambda\left(\sup_{t>0} \operatorname{dist}(x(t;x_0,\eta_\lambda),A) \leq \delta\right) = 1.$$

In particular, if η_λ is deterministic (e.g., an exogenous disturbance), we can omit $\mathbb{P}_\lambda$ and reinterpret $(\infty, 1, \delta, \delta)$-resilience as $x(t; x_0, \eta_\lambda) \in A_\delta$ for all $t > 0$ and $\lambda \in \mathcal{I} \setminus \{\lambda_0\}$. In comparison to the definition of A being a *robust* attractor for the trajectories $x(t; x_0, \eta_\lambda)$ of the family $\mathcal{F}$, as per Definition 1, $(\infty, 1, \delta, \delta)$-resilience of the family means that for any *deterministic* perturbation, the state $x(t; x_0, \eta_\lambda)$ remains in A_δ for all $t > 0$: no deterministic perturbation in the family $\mathcal{F}$ can drive the state away from a δ-neighbourhood of A.

The next definition allows the system state $x(t; x_0, \eta_\lambda)$ to exhibit weak oscillations and arbitrarily large detours away from the attractor A.

Definition 3. (Asymptotic practical resilience). Consider a family of systems $\mathcal{F} = \{G_\lambda\}_{\lambda \in \mathcal{I}}$ and let $(A, B(A))$ be an attractor-basin pair corresponding to G_{λ_0}. Let the distance $\delta \in [0, \infty)$ and the confidence level $\gamma \in (0, 1]$ be fixed. The system G_λ is (γ, δ)-*asymptotically practically resilient* if, for all $x_0 \in B(A)$,

$$\mathbb{P}_\lambda \left(\limsup_{t \to \infty} \operatorname{dist}(x(t; x_0, \eta_\lambda), A) \leq \delta \right) \geq \gamma.$$

The family $\mathcal{F}$ is (γ, δ)-*asymptotically practically resilient* if, for all $x_0 \in B(A)$,

$$\inf_{\lambda \in \mathcal{I} \setminus \{\lambda_0\}} \mathbb{P}_\lambda \left(\limsup_{t \to \infty} \operatorname{dist}(x(t; x_0, \eta_\lambda), A) \leq \delta \right) \geq \gamma.$$

When $\delta = 0$, we say that the system (respectively, the family) is γ-*asymptotically resilient.*

Remark 1. When $\delta = 0$ and $\gamma = 1$, Definition 3 of asymptotic resilience reduces to robustness of the property $\mathcal{P}$ in (6) according to (7).

Differently from Definition 2, which deals with the transient behaviour of the system trajectories, Definition 3 deals with their asymptotic properties and requires the trajectories emanating from $x_0 \in B(A)$ to converge to a δ-neighbourhood of the attractor A with probability at least $\gamma > 0$.

The efficacy of the proposed definitions is demonstrated in Section 3, by considering their application to Examples 1 and 2 in Section 2.1.

Remark 2. The proposed definitions of resilience heavily rely on the structure of the family $\mathcal{F}$. In particular, the attractor-basin pair $(A, B(A))$ is determined (and fixed) by reference to the nominal deterministic system G_{λ_0}. The resilience of G_λ for $\lambda \neq \lambda_0$ is then determined by relating the behaviour of the trajectories $x(t; x_0, \eta_\lambda)$ to a neighbourhood of A. Consider, for example, Definition 3 for $\lambda \neq \lambda_0$. Even when η_λ is deterministic, its addition to the right-hand side of the ODEs may alter the attractor A to a new attractor $A(\lambda)$, which will be close to A, subject to appropriate assumptions on η_λ. Hence, allowing for $\delta > 0$ in Definition 3 is essential to obtain a meaningful definition. An alternative approach to defining resilience would be to require the *property of existence of an attractor-basin pair* (which may be different from the pair $(A, B(A))$, induced by the nominal system G_{λ_0}) to be preserved, with high enough probability. This is a valid alternative approach, which is outside the scope of the current paper, and is left for future investigation.

2.3 Attraction time as a resilience indicator

As a specific resilience indicator (see e.g. Dakos et al. (2015) for an introduction to the topic), we consider the *attraction time* of a system, which probabilistically quantifies the time it takes for a perturbed/noisy system to reach a neighbourhood of a prescribed equilibrium state. Here, we show how such an indicator can be formally defined for the considered family of systems (see Section 2.1), relying on Definition 3.

Definition 4. Consider the family $\mathcal{F} = \{G_\lambda\}_{\lambda \in \mathcal{I}}$. Let $\lambda \neq \lambda_0$ and assume that G_λ is (γ, δ)-asymptotically practically resilient. Let $x_0 \in B(A)$, $\nu \in [0, \infty)$, $\tau \in (0, \infty)$ and $\mu \in (0, 1]$. Then, the system G_λ has a (τ, μ, ν)-*attraction time* with respect to x_0 if

$$\mathbb{P}_\lambda \left(\sup_{t \in [\tau, \infty)} \operatorname{dist}(x(t; x_0, \eta_\lambda), A) \leq \nu \right) \geq \mu.$$

Similarly, given $x_0 \in B(A)$, the family $\mathcal{F}$ has a (τ, μ, ν)-*attraction time* with respect to x_0 if

$$\inf_{\lambda \in \mathcal{I} \setminus \{\lambda_0\}} \mathbb{P}_\lambda \left(\sup_{t \in [\tau, \infty)} \operatorname{dist}(x(t; x_0, \eta_\lambda), A) \leq \nu \right) \geq \mu.$$

In words, G_λ has a (τ, μ, ν)-*attraction time* if the probability of the state to return to a ν-neighbourhood of the attractor A after time τ is at least μ. Note that, given ν, smaller τ and/or larger μ for which G_λ has (τ, μ, ν)-attraction time imply higher resilience of the attractor A of G_{λ_0} when the dynamics is perturbed by η_λ.

The next proposition shows that the notion of attraction time is well-defined.

Proposition 1. Let G_λ be (γ, δ)-asymptotically practically resilient for $x_0 \in B(A)$ and some $\delta \in [0, \infty), \gamma \in (0, 1]$. Then, there exist some $\nu, \tau \in (0, \infty)$ and $\mu \in (0, 1)$ such that G_λ has a (τ, μ, ν)-*attraction time.*

Proof 1. Choose $\nu > \delta$ and define the following sets

$$E_0 = \left\{ \limsup_{t \to \infty} \operatorname{dist}(x(t; x_0, \eta_\lambda), A) \leq \delta \right\},$$
$$E_n = \left\{ \sup_{t \geq n} \operatorname{dist}(x(t; x_0, \eta_\lambda), A) \leq \nu \right\}.$$

By definition of the limit superior, $E_0 \subset \bigcup_{n \in \mathbb{N}} E_n$. Also, $E_n \subseteq E_{n+1}$ for all $n \in \mathbb{N}$. Hence, by monotone convergence

$$\gamma \leq \mathbb{P}_\lambda(E_0) = \lim_{n \to \infty} \mathbb{P}_\lambda (E_0 \cap E_n) \leq \lim_{n \to \infty} \mathbb{P}_\lambda(E_n).$$

Hence, for any $0 < \zeta < 1$, there exists a sufficiently large n such that G_λ has a $(n, \zeta\gamma, \nu)$-attraction time.

3. NUMERICAL EXAMPLES

3.1 Example 1: Turing patterns

We consider Example 1 from Section 2.1 to illustrate how resilience definitions can quantify the sensitivity of a model to noise and initial conditions, over its dynamical evolution. As discussed by Bashkirtseva et al. (2021), the deterministic Levin-Segel model (3) exhibits regions of multistability, where patterns may temporarily form but ultimately dissipate and other stable structures emerge, with the limit case of spatially homogeneous equilibrium values $(\bar{u}, \bar{v}) = \left(\frac{ad}{bc-de}, \frac{ac}{bc-de} \right)$ when $D_u = D_v = 0$. Noise may further alter the picture, yielding alternative patterns during the time evolution. Practical resilience and attraction time provide summary statistics to quantitatively compare different scenarios. Consider the stable pattern in Fig. 4, obtained through the Crank-Nicolson numerical scheme applied to (3) with Neumann boundary conditions, $\lambda = \lambda_0 = 0$, $a = d = e = 0.5$, $b = c = 1$, $D_v = 0.005$, $D_u = 1.4 \cdot 10^{-4}$, spatial step $dx = 0.01$ and time step $dt = 0.01$ over a rectangle with spatial length $L = 1$ and time horizon $t_{fin} = 250$ s.

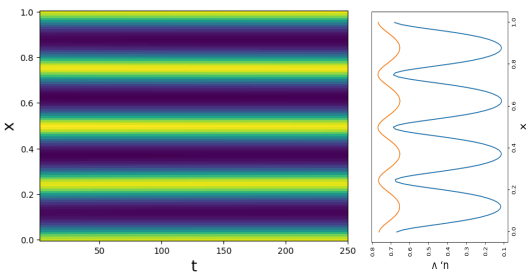

Fig. 4. Left: Turing-pattern attractor corresponding to u from the deterministic system (3) with $\lambda = \lambda_0 = 0$, visualised over space x and time t, with the parameter values described in the main text. Right: Turing-pattern attractor for u, blue, and v, orange.

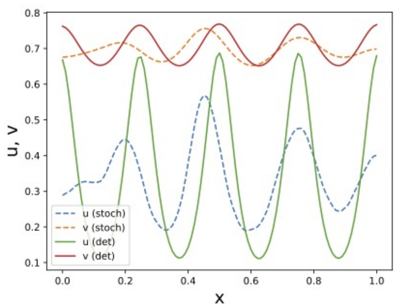

Fig. 5. Realisations of states $u(t, \cdot)$ and $v(t, \cdot)$ of system (3), with $t = 250$ s, in the deterministic case $\lambda = \lambda_0 = 0$ (solid) and in the stochastic case $\lambda = 40 \cdot 10^{-4}$ (dashed), with the other parameter values described in the main text.

Initial conditions within $\pm\delta$ distance from the Turing-pattern attractor, as well as noise levels λ, alter the system state at each time point (see e.g. Fig. 5). Practical resilience (Definition 2) with $\varepsilon = \delta$ and attraction time (Definition 4) allow to identify up to which distance levels δ (uniform over the spatial grid) the Turing patterns can be considered resilient, depending on the noise intensity λ. Table 1 reports selected case studies. For low levels of λ, the system state may remain within distance δ from the deterministic Turing-pattern attractor, with a probability $\mathbb{P}_\lambda$ that increases for larger δ, as expected. However, increasing λ disrupts the patterns and drives the states away from the attractor. Using the attraction time as a resilience indicator offers a consistent insight. We compute the worst-case attraction time over all the simulated initial conditions. As can be seen in Table 1, τ is smaller when the corresponding probability is larger, and *vice versa*; the indication '$-$' for τ denotes settings for which asymptotic practical resilience was not achieved within the simulation horizon $t_{fin} = 250$ s. Overall, this analysis allows to identify *probabilistic* performance guarantees, beyond robustness analysis, according to a desired confidence level γ.

	δ (for $\mathbb{P}_\lambda$)			δ (for $\tau[s]$)		
$\lambda\,(\cdot\mathbf{10^{-4}})$	0.01	0.05	0.1	0.01	0.05	0.1
1	0.125	0.875	0.958	200	85	61
9	0	0	0.5	-	-	162
25	0	0	0	-	-	-
40	0	0	0	-	-	-

Table 1. Values of $\mathbb{P}_\lambda$ (center) and of the worst-case attraction time τ (right) for given choices of the distance δ and of the noise intensity λ, for system (3) with parameter values as in the main text.

3.2 Example 2: gene regulatory network

For Example 2 from Section 2.1, we now assess $(\tau, \gamma, \delta, \delta)$-practical resilience. To this end, we perform numerical simulations of the system (5) around the stable equilibrium $\mathbf{x}_3$ (see Fig. 6), for uniformly spaced initial conditions $x_0 \in (\mathbf{x}_3 - \delta; \mathbf{x}_3 + \delta)$, and assess whether the trajectories lie within $(\mathbf{x}_3 - \delta; \mathbf{x}_3 + \delta)$ over a finite horizon t_{fin}, for a range of noise intensities λ.

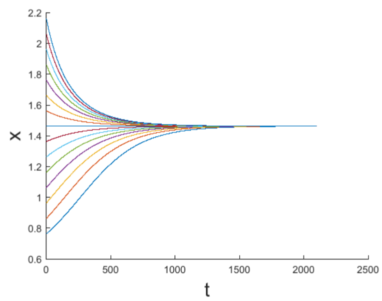

Fig. 6. Trajectories for the nominal system (1), converging to a stable state $\mathbf{x}_3$ for a range of initial conditions x_0 in a δ-neighbourhood of the attractor.

We consider different values of the distance $\delta \in [\delta_{min}, \delta_{max}]$, with $\delta_{min} = 0.05\mathbf{x}_3$ and $\delta_{max} = |\mathbf{x}_3 - \mathbf{x}_2|$, which is the distance from the unstable equilibrium $\mathbf{x}_2$. Fig. 7 shows the values of $\mathbb{P}_\lambda$ depending on δ and λ: as expected, the probability of remaining within a δ-neighbourhood of the attractor is larger if δ is larger and if the noise intensity λ is smaller. Setting the desired γ threshold for $\mathbb{P}_\lambda$ identifies specific resilience levels.

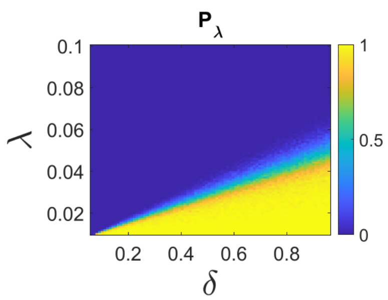

Fig. 7. Dependence of $\mathbb{P}_\lambda$ on δ and λ for the stochastic gene regulation model (5) with $k = 0.1$, $h = 2$ and $a = 2$ (within the bistable region shown in Fig. 2).

Considering the worst-case attraction time τ (over all simulated initial conditions) as a resilience metric yields the values shown in Fig. 8. For system (5), τ is computed by setting $\nu = \delta$ and $\mu = 1$, for each of the values of δ and λ considered above. As shown by comparing

Fig. 7 and Fig. 8, the region with high values of $\mathbb{P}_\lambda$ (close to 1) is correlated with smaller values of the worst-case attraction time. The upper bound on τ in Fig. 8 designates the simulation horizon t_f and identifies cases where asymptotic practical resilience was not observed.

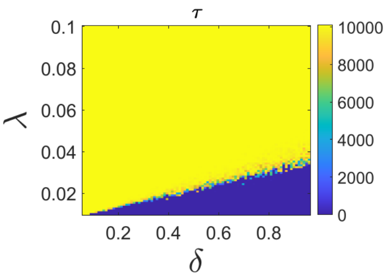

Fig. 8. Worst-case attraction time τ for different δ and λ for system (5) with $k = 0.1$, $h = 2$ and $a = 2$.

Simulations so far demonstrated the definitions for prescribed values of the system parameters. The deterministic model (1) with fixed $k = 0.1$ and $h = 2$ exhibits a bifurcation when $a = a_{c,1}$. It is of interest to understand how proximity of a to $a_{c,1}$ affects the resilience of the perturbed stochastic system G_λ in (5). To this end, we study $(\infty, \cdot, \delta(a), \delta(a))$-practical resilience, where $\delta(a) = |\mathbf{x}_3(a) - \mathbf{x}_2(a)|$ and $a \in (a_{c,1}; a_{max})$. Here, $a_{c,1} \approx 1.77$ corresponds to the lower bifurcation value (see Fig. 2) and $a_{max} \approx 1.89 < a_{c_2} \approx 2.63$ is within the bistable parameter region, while $\mathbf{x}_3(a)$ is a stable equilibrium and $\mathbf{x}_2(a)$ is the unstable equilibrium (see Fig. 1). The values of the probability $\mathbb{P}_\lambda$ are given in Fig. 9. The perturbed system trajectories reside within a $\delta(a)$-neighbourhood of $\mathbf{x}_3(a)$ when the bifurcation parameter a is sufficiently far from $a_{c,1}$, for all simulated noise intensities. However, as a tends to $a_{c,1}$, the probability associated with practical resilience decreases sharply. Specifying a desired γ then allows one to identify regions of interest where practical resilience holds.

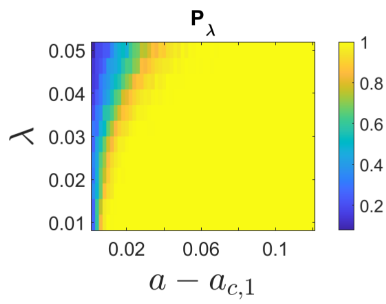

Fig. 9. Dependence of $\mathbb{P}_\lambda$ on λ and $a - a_{c,1}$, where $a_{c,1}$ is the lower bifurcation value, for system (5) with $k = 0.1$ and $h = 2$.

4. CONCLUSION

Motivated by applications in systems biology, we introduced definitions of resilience for a class of stochastic dynamical systems, to complement previous notions of robustness. Our definitions allow for a quantitative probabilistic assessment of the impact of noise on desired system properties, related to the preservation of an attractor. Furthermore, the proposed concepts allow to formally define the attraction time as a rigorous resilience indicator. We show how our definitions can be applied to gain insight into the behaviour of widely used biological systems.

Future work will include the application of the proposed framework to the numerical and analytical study of complex systems subject to parametric uncertainties and stochastic disturbances. This study also paves the way to the design of additional resilience indicators. Moreover, it would be interesting to explore the connection between the proposed definitions and a stochastic version of the stability radius (Hinrichsen and Pritchard, 2005), which may allow for further quantification of resilience.

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