

Structural stability of nonlinear population dynamics

Simone Cenci and Serguei Saavedra*

Department of Civil and Environmental Engineering, MIT, 77 Massachusetts Avenue, Cambridge, Massachusetts 02139, USA

(Received 23 October 2017; published 11 January 2018)

In population dynamics, the concept of structural stability has been used to quantify the tolerance of a system to environmental perturbations. Yet, measuring the structural stability of nonlinear dynamical systems remains a challenging task. Focusing on the classic Lotka-Volterra dynamics, because of the linearity of the functional response, it has been possible to measure the conditions compatible with a structurally stable system. However, the functional response of biological communities is not always well approximated by deterministic linear functions. Thus, it is unclear the extent to which this linear approach can be generalized to other population dynamics models. Here, we show that the same approach used to investigate the classic Lotka-Volterra dynamics, which is called the structural approach, can be applied to a much larger class of nonlinear models. This class covers a large number of nonlinear functional responses that have been intensively investigated both theoretically and experimentally. We also investigate the applicability of the structural approach to stochastic dynamical systems and we provide a measure of structural stability for finite populations. Overall, we show that the structural approach can provide reliable and tractable information about the qualitative behavior of many nonlinear dynamical systems.

DOI: [10.1103/PhysRevE.97.012401](https://doi.org/10.1103/PhysRevE.97.012401)**I. INTRODUCTION**

Quantifying the tolerance of interacting populations to environmental perturbations has been the center of theoretical population-biology research for many decades [1–3]. The big challenges behind this task are the difficulty in producing a large number of exact experimental replicates on which to test theories, the analytical intractability of complex mechanistic models, and the possibility that the functional form of the model itself can change throughout time [3,4]. In order to deal with these challenges, a typical approach is to focus on simple yet insightful models derived from first principles [5]. However, while simple models of population dynamics can be tractable, they are often criticized for providing a nonrealistic deterministic version of the factors shaping the time evolution of population abundances [6]. The classic example of a simple deterministic model that has attracted much attention, but that has been strongly criticized, is the Lotka-Volterra (LV) model [7,8]. While this model has been derived from thermodynamics principles [9], from principles of conservation of mass and energy [5], from chemical kinetics in large populations [10], and can exhibit a rich behavior such as chaotic dynamics [11] and limit cycles [12], it seems unreasonable to believe that such a simple deterministic model could describe the time evolution of population abundances that we observe in nature [6].

Certainly, despite its mechanistic foundation, the classic LV dynamics does not take into account many important biological and environmental processes ranging from fluctuations in birth and death processes to saturating effects of species growth [5]. In order to deal with some of these limitations, recent theoretical work has developed structural approaches that are based on

the concept of structural stability [2,13]—that is, stability of the qualitative behavior of a dynamical system against fluctuations of its parameters [14,15]. Following a structural approach, studies have been able to reconcile foundational hypotheses in ecology with observational data [14,16–18]. Importantly, here we show that this approach can be directly applied to a larger class of population dynamics models with nonlinear functional responses. The main implication of our findings is that the applicability of the structural approach does not depend exclusively on the assumption of pairwise interactions or that dynamics are generated by one single deterministic model whose functional form remains fixed in time. We also show how to extend the approach to investigate the structural stability of stochastic dynamics.

The paper is organized as follows. In the Sec. II, we briefly review the details of the structural approach focusing on its geometrical interpretation. In Sec. III, we derive the conditions under which we can apply the structural approach to study the structural stability of nonlinear population dynamics. In Sec. IV, we examine the applicability of this approach to stochastic dynamical systems focusing on the stochastic LV model. Finally, in Sec. V, we discuss the implications of our findings.

II. BACKGROUND: STRUCTURAL APPROACH

The structural approach is a geometric methodology recently introduced [14,15,19] to provide a quantitative measure for the structural stability of the classic LV dynamics:

$$\dot{\vec{x}} = \vec{x}(\vec{r} - \mathcal{A}\vec{x}), \quad (1)$$

where \vec{x} is the vector of population abundances (i.e., the state variables), \vec{r} is the vector of intrinsic growth rates (i.e., the difference between death and birth rate), \mathcal{A} is the $d \times d$ interaction matrix, and d is the dimension of the state space

*Author to whom correspondence should be addressed: sersaa@mit.edu

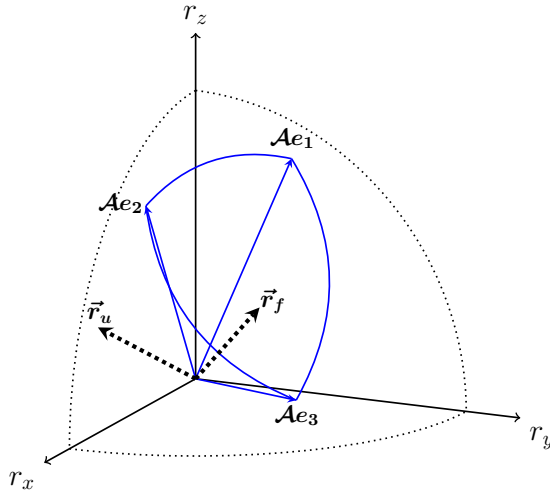


FIG. 1. Structural approach to infer the structural stability of feasible fixed points in the classic Lotka-Volterra dynamics. The figure shows the feasibility domain in the parameter space of the intrinsic growth rates. A fixed point of the classic LV dynamics is feasible if the vector of intrinsic growth rates falls within the feasibility domain spanned by the columns of the interaction matrix \mathcal{A} , such as the vector \vec{r}_f illustrated in the figure. Otherwise, a vector \vec{r}_u would generate an unfeasible solution, i.e., one or more species would be extinct at the fixed point. The structural approach uses the size of the feasibility domain as a measure for the structural stability of the feasible fixed point.

(i.e., the number of species). The classic LV dynamics is a deterministic model derived from the infinite population limit of a multispecies stochastic process with mass action assumption on the transition rates [20,21].

A dynamical system is said to be structurally stable if smooth variations of the model (e.g., its parameters) leave some properties of the system unchanged [22]. For example, hyperbolic dynamical systems are a typical case of structurally stable models [23]. Additionally, structural stability has a geometrical interpretation. That is, the parameter space of structurally stable dynamical systems can be partitioned into structurally stable domains separated by regions that are structurally unstable [24]. Within the structurally stable domains, smooth changes of the parameters (caused for example by environmental perturbations) do not change the nature of the fixed point. For instance, if a fixed point of a dynamical system exists and is feasible (i.e., all species have positive abundances on the attractor), perturbations that keep the parameters within the structurally stable domains preserve its feasibility.

The structural approach uses the size of the structurally stable domains of feasible fixed points as a measure for the structural stability of the population dynamics model [14,15,19]. This domain is known as the feasibility domain [5,14], i.e., a convex region within the parameter space of a dynamical system from which it is possible to sample parameters that generate feasible solutions. The larger the feasibility domain, the larger the structural stability of a feasible fixed point (see Fig. 1). Formally, for classic LV dynamics, because of the linearity of the functional response, the feasibility domain is a convex hull in the parameter space

of the intrinsic growth rates \vec{r} spanned by the columns of the interaction matrix \mathcal{A} :

$$D_F(\mathcal{A}) = \left\{ \vec{r} \in \mathbb{R}^d \mid \exists \lambda_1, \dots, \lambda_d > 0, r_j = \sum_i \lambda_i a_{ij} \right\}. \quad (2)$$

A fixed point is feasible if the vector of intrinsic growth rates lies within the feasibility domain [5] (see Fig. 1 for a graphical example). In fact, by considering a nonsingular interaction matrix \mathcal{A} , the vector of state variables can be rewritten as a combination of a standard basis of \mathbb{R}^d , i.e., $\vec{x} = x_1 e_1 + \dots + x_n e_n$ and $\mathcal{A}\vec{x} = \sum_j x_j \mathcal{A}e_j$. Therefore the positive orthant (i.e., the state space of LV) is contracted to a n -hedral angle with generatrices formed by the columns of the interaction matrix. Hence a feasible (positive) solution of $\mathcal{A}\vec{x} = \vec{r}$ exists if $\vec{r} \in D_F(\mathcal{A})$ [5,14]. This is precisely the nonzero fixed point of Eq. (1).

Following the structural approach [14,15], the structural stability of the classic LV dynamics can be quantified by measuring the volume of the feasibility domain in the L_p norm: $\Omega = \frac{|\det \mathcal{A}|}{\|\mathcal{A}e_1\|_{L_p} \dots \|\mathcal{A}e_d\|_{L_p}}$, where d is the dimension of the system. The choice of the norm or the normalization factors of the interaction matrix does not change the computation of the volume [5,19]. Particularly, the relevance of the feasibility domain relies on its quantitative characterization of structural stability and its conceptual interpretation as the tolerance of a dynamical system to environmental perturbations [15,17,25].

III. GENERALIZATION TO NONLINEAR FUNCTIONAL RESPONSES

One important question that remains to be answered is to which other models the structural approach can be extended. To answer this question, let us consider a more general form for the classic LV dynamics:

$$\dot{\vec{x}} = \vec{x}[\vec{r} - \mathcal{A}f(\vec{x})], \quad (3)$$

where $f(\vec{x})$ denotes a general functional response. This type of model has been typically called generalized Lotka-Volterra (GLV), and their association with the classic LV dynamics has been extensively studied [26]. For example, under classic LV dynamics, the non-negative equilibrium point is the solution to the linear complementary problem (LCP) for \mathcal{A} and \vec{r} [i.e., $\text{LCP}(\mathcal{A}, -\vec{r})$]. Similarly, the non-negative equilibrium point of GLV is the solution to the nonlinear complementary problem (NCP) for $\mathcal{A}f(\vec{x})$ and \vec{r} [i.e., $\text{NCP}(\mathcal{A}f(\vec{x}), -\vec{r})$]. It is also known that if $f(\vec{x})$ is continuous and monotone in \mathbb{R}^d , then there exists a non-negative equilibrium of Eq. (3) for some $\vec{r} \in \mathbb{R}^d$. Importantly, these associations allow us to be more concrete and redefine the question above to whether it is possible to apply the structural approach to study the structural stability of the feasible fixed point of Eq. (3).

Here, we derive the sufficient conditions for the applicability of the structural approach to Eq. (3). We do this by mapping the nonlinear functional response into a linear response and finding the conditions for $f(\vec{x})$ under which this change of variable leaves the state space of Eq. (3) unchanged. Then, we ensure that the system in the new variable is topologically equivalent to LV. Formally, let us call $\vec{z} = f(\vec{x})$. Then,

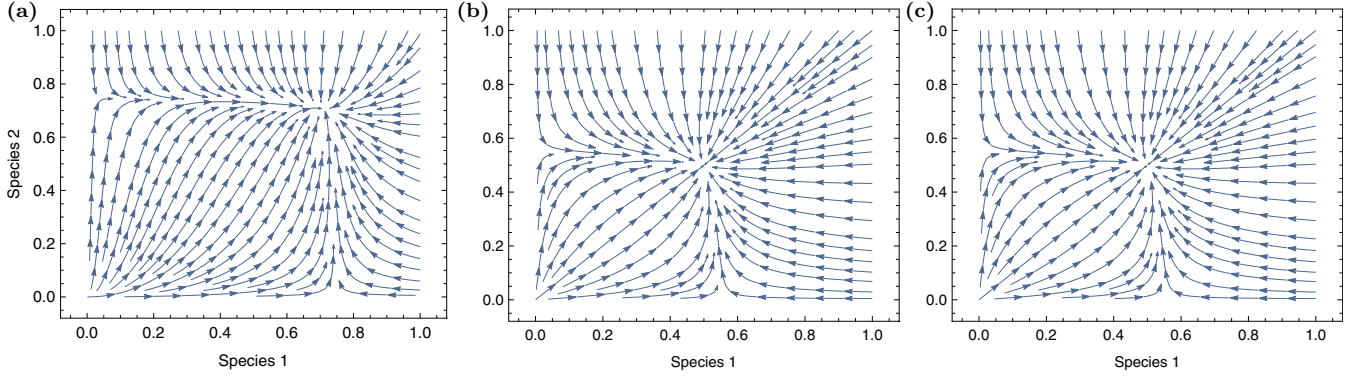


FIG. 2. Topological equivalence between classic and generalized Lotka-Volterra dynamics for a polynomial response function. Panel (a) shows the direction field of Eq. (3) with a polynomial response function, i.e., $f(\vec{x}) = \vec{x}^2$. Panel (b) shows the direction field of the linear transformation of GLV dynamics, as given by Eq. (8) with $\beta = 2$. As a reference, panel (c) shows the direction field of the classic LV dynamics, i.e., Eq. (1). The figure shows that the state spaces are equivalent. Note that changing the exponent of the polynomial would just modify the qualitative picture of the state space but would leave the structure of the state space unchanged. The polynomial response function satisfies the conditions in Eq. (6). Parameters: $r_i = 0.5$, $\mathcal{A}_{ii} = 0.9$, and $\mathcal{A}_{ij} = 0.1$

$$\vec{x} = f^{-1}(\vec{z}):$$

$$\dot{\vec{x}} = \vec{x}[\vec{r} - \mathcal{A}f(\vec{x})] \Rightarrow \frac{d[f^{-1}(\vec{z})]}{dt} = f^{-1}(\vec{z})(\vec{r} - \mathcal{A}\vec{z}), \quad (4)$$

which can be rewritten as

$$\frac{d\vec{z}}{dt} = \frac{1}{\nabla[f^{-1}(\vec{z})]} f^{-1}(\vec{z})(\vec{r} - \mathcal{A}\vec{z}). \quad (5)$$

Because we are interested in a feasible fixed point, we need to guarantee that the inverse of the transformation must map points in the state space \mathcal{S} of Eq. (5) to points in the positive orthant of the original dynamical system of Eq. (3) (i.e., $f^{-1} : \mathcal{S} \subseteq \mathbb{R}_{>0}^d \rightarrow \mathbb{R}_{\geq 0}^d$). The topological equivalence to the classic LV dynamics also implies that Eq. (3) and Eq. (5) must have only two fixed points in \mathcal{S} : one feasible stable point and one feasible (or unfeasible) unstable point. Thus, the change of variable also must map the unstable fixed point of Eq. (3) onto the unstable fixed point of Eq. (5) and the same for the stable one. Specifically, this translates into requiring the condition that $\frac{f^{-1}(\vec{z})}{\nabla[f^{-1}(\vec{z})]}$ is well defined in \mathcal{S} (i.e., $\nabla[f^{-1}(\vec{z})] \neq 0$) and that its (only) root is an unstable fixed point of Eq. (5). Formally, the conditions under which we can consider Eq. (3) and Eq. (5) to be topologically equivalent to the classic LV can be written as

$$\begin{aligned} \exists! \vec{x} \in \mathbb{R}_{>0}^d \mid \vec{r} - \mathcal{A}f(\vec{x}) = 0, \quad f^{-1} : \mathcal{S} \subseteq \mathbb{R}_{>0}^d \rightarrow \mathbb{R}_{\geq 0}^d, \\ \exists! \vec{z}^* \in \mathbb{R}_{\geq 0}^d \mid \frac{f^{-1}(\vec{z}^*)}{\nabla[f^{-1}(\vec{z}^*)]} = 0, \end{aligned} \quad (6)$$

where \vec{z}^* is an unstable fixed point of Eq. (5). Note that the first two conditions derive directly from previous results on GLV dynamics [26]. To illustrate the conditions of Eq. (6), let us consider a practical example. If we take $f(\vec{x}) = \vec{x}^\beta \Rightarrow \vec{x} = \vec{z}^{1/\beta}$,

$$\dot{\vec{x}} = \vec{x}(\vec{r} - \mathcal{A}\vec{x}^\beta), \quad (7)$$

$$\dot{\vec{z}} = \beta\vec{z}(\vec{r} - \mathcal{A}\vec{z}), \quad (8)$$

then a feasible solution of Eq. (8) guarantees the feasibility of Eq. (7) given that the inverse function f^{-1} maps each point onto the positive orthant of Eq. (8) to the positive orthant of the original system. Furthermore, because the system \vec{z} has a linear stationary state (see Fig. 2), we can apply the structural approach to Eq. (8) to measure the structural stability of the fixed point of Eq. (7).

Following the rationale above, we can generalize our results beyond GLV dynamics. To illustrate this, let us now consider the following general population dynamics model:

$$\dot{\vec{x}} = g(\vec{x})[\vec{r} - \mathcal{A}f(\vec{x})]. \quad (9)$$

Using the change of variable $\vec{z} = f(\vec{x})$, we can rewrite Eq. (9) as

$$\frac{d\vec{z}}{dt} = \frac{1}{\nabla[f^{-1}(\vec{z})]} g[f^{-1}(\vec{z})](\vec{r} - \mathcal{A}\vec{z}). \quad (10)$$

We call \mathcal{S}_1 and \mathcal{S}_2 the state spaces of Eq. (9) and Eq. (10), respectively. Note that \mathcal{S}_1 is not necessarily the entire positive orthant, but we continue to assume that the function $g(\vec{x})$ has at most one zero in \mathcal{S}_1 and it is an unstable fixed point of Eq. (9). It is now straightforward to see that the conditions leading to topological equivalence are (1) the system $\vec{r} - \mathcal{A}f(\vec{x}) = 0$ has only one solution in the positive orthant, (2) $f^{-1} : \mathcal{S}_2 \subseteq \mathbb{R}_{>0}^d \rightarrow \mathcal{S}_1$, and (3) $\frac{g[f^{-1}(\vec{z})]}{\nabla[f^{-1}(\vec{z})]}$ has at most one root in \mathcal{S}_2 . This last condition needs to be satisfied given that we have imposed that $g(\vec{x})$ has only one root.

In sum, in this section, we have provided the sufficient conditions that need to be assumed in a response function in order to study the structural stability of nonlinear models under the structural approach derived for linear functional responses. As a final note, we want to stress that the conditions in Eq. (6) are sufficient but not necessary. To illustrate this point, let us consider the case of a functional response of type II, that is $f_{ii}(\vec{x}) = \mathcal{M}\vec{x}$, where \mathcal{M} is a diagonal matrix with diagonal entries $\mathcal{M}_{ii} = \frac{1}{1+x_i}$. For this type of functional response the conditions in Eq. (6) are not satisfied. Specifically, because $\vec{z} \in \mathbb{R}_{\geq 0}^d$, then $f^{-1} : \mathbb{R}_{\geq 0}^d \rightarrow \mathbb{R}^d$ and there also exists an additional feasible fixed point which is not globally (and

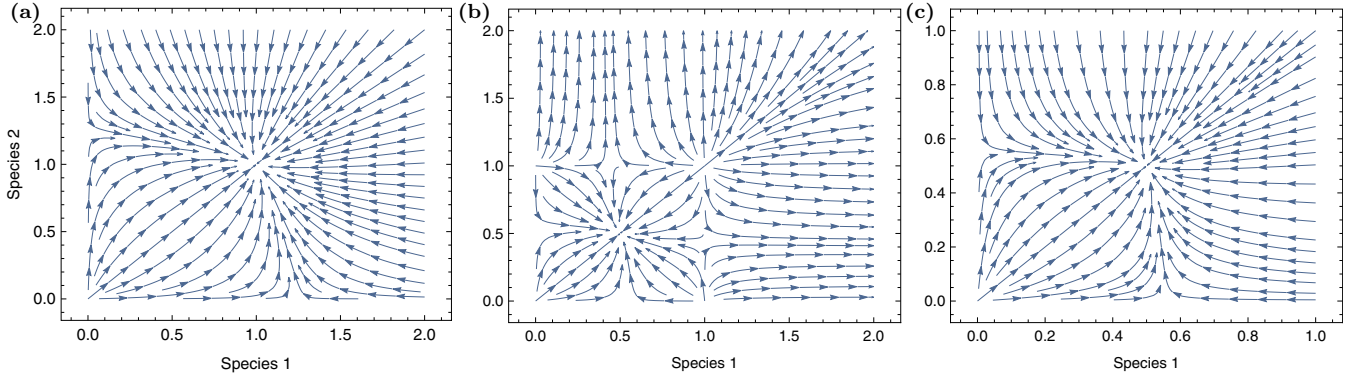


FIG. 3. Direction field of Lotka-Volterra dynamics with a functional response of type II. While the state space of Eq. (9) with a functional response of type II (a) is mapped into a state space that is not topologically equivalent to LV (b), the restriction of this state space on the basin of attraction $\mathcal{B} = [0,1) \times [0,1)$ of the stable fixed point is. As a reference, panel (c) shows the direction field of the classic LV dynamics. Parameters: $r_i = 0.5$, $\mathcal{A}_{ii} = 0.9$, and $\mathcal{A}_{ij} = 0.1$.

locally) stable. Nevertheless, it has already been shown that the structural approach can still be applied to these types of functional responses [15]. As illustrated in Fig. 3, the basin of attraction of the only stable fixed point is the only subregion of \mathcal{S}_2 that can be mapped back into the positive orthant of the original system. The basin of attraction of this feasible stable fixed point (plus the origin) is, indeed, topologically equivalent to the classic LV dynamics. This example suggests that (1) if there exists a basin of attraction \mathcal{B} of the stable fixed point of Eq. (10) topologically equivalent to LV, and (2) this is the only subregion of \mathcal{S}_2 that is mapped back by f^{-1} to \mathcal{S}_1 , then we can still apply the structural approach to the restriction of the state space on \mathcal{B} . These results imply that we can relax the conditions in Eq. (6), and extend the validity of the structural approach to a much larger class of functional responses if there exists a unique subregion of the state space of Eq. (10) for which the conditions in Eq. (6) hold.

IV. STRUCTURAL STABILITY OF STOCHASTIC DYNAMICS

The analysis in the previous section was limited to deterministic dynamical systems. This is a good approximation in the limit of infinitely large populations. However, when this limit cannot be assumed, noise in the state variables (i.e., demographic stochasticity) cannot be neglected. That is, fluctuations of the state variables need to be considered explicitly. In this section, we show under which conditions we can study the structural stability of stochastic LV dynamics (SLV) under the structural approach derived for linear functional responses. Then, we introduce an extension of the structural approach to take into account the extinction probability in finite populations.

The SLV can be derived from the linear noise approximation (LNA) of the chemical master equation [27,28] for the probability distribution of the stochastic process that generate the classic LV dynamics. In terms of chemical kinetics, this stochastic process is typically defined as $X \rightarrow \emptyset$, $X \rightarrow X + X$, and $X + Y \rightarrow X$, where X and Y stand for species X and species Y [10,20]. Within this framework, the SLV dynamics

then reads [20]

$$\dot{\vec{x}} = \vec{x}(\vec{r} - \mathcal{A}\vec{x}) + \frac{1}{\sqrt{N}}\nu(t), \quad (11)$$

where the first term on the right hand side is the deterministic vector field, N is the system size, and $\nu(t)$ is Gaussian white noise [29] with zero mean and correlations given by $\langle \nu_i(t)\nu_j(t') \rangle = \mathcal{B}_{ij}\delta(t-t')$, where $\mathcal{B}_{ij} = \vec{x}(\vec{r} + \mathcal{A}\vec{x}) \forall i = j$ and zero otherwise. The δ function in the last expression characterizes the white noise.

Here we ask whether we can apply the structural approach to finite populations, i.e., to Eq. (11). For globally stable systems, because the dynamics away from the fixed point are dominated by the deterministic component, the deterministic vector field pushes back the perturbations induced by stochastic fluctuations of the state variables to the feasible solution. Nevertheless, note that the extinction probability is always different from zero because the system size is finite. That is, globally stable fixed points are only metastable since demographic stochasticity will eventually induce a transition into an absorbing state [30]. Generally, the smaller the system size, the larger the extinction probability. However, the time for extinction T_{ext} due to stochastic fluctuations is typically very large, and in globally stable SLV systems this time scales as $T_{\text{ext}} \propto e^N$ [31]. Note that N is finite but assumed to be large, hence T_{ext} can be regarded as infinity for practical purposes. Thus, in this limit, the structural approach can be applied to globally stable SLV systems.

However, recently it has been shown that in neutral and quasineutral conditions, the argument provided above does not hold anymore [20,31,32]. Specifically, the extinction time for neutrally stable SLV models scales proportionally to the system size N , i.e., $T_{\text{ext,neut}} \sim N^\alpha$ rather than exponentially [30,31,33]. The reason for this change in behavior of the system is that, near neutrality, there exists a new dynamics on the center (CM) and slow (SM) manifold of SLV, that cannot be studied in the deterministic setting. That is, extinctions of species in time proportional to $T_{\text{ext,neut}}$ are driven by a stochastic drift on the CM or the SM [20,32].

Importantly, the existence of a center manifold is a hallmark of *structural instability* given that the dominant eigenvalue of

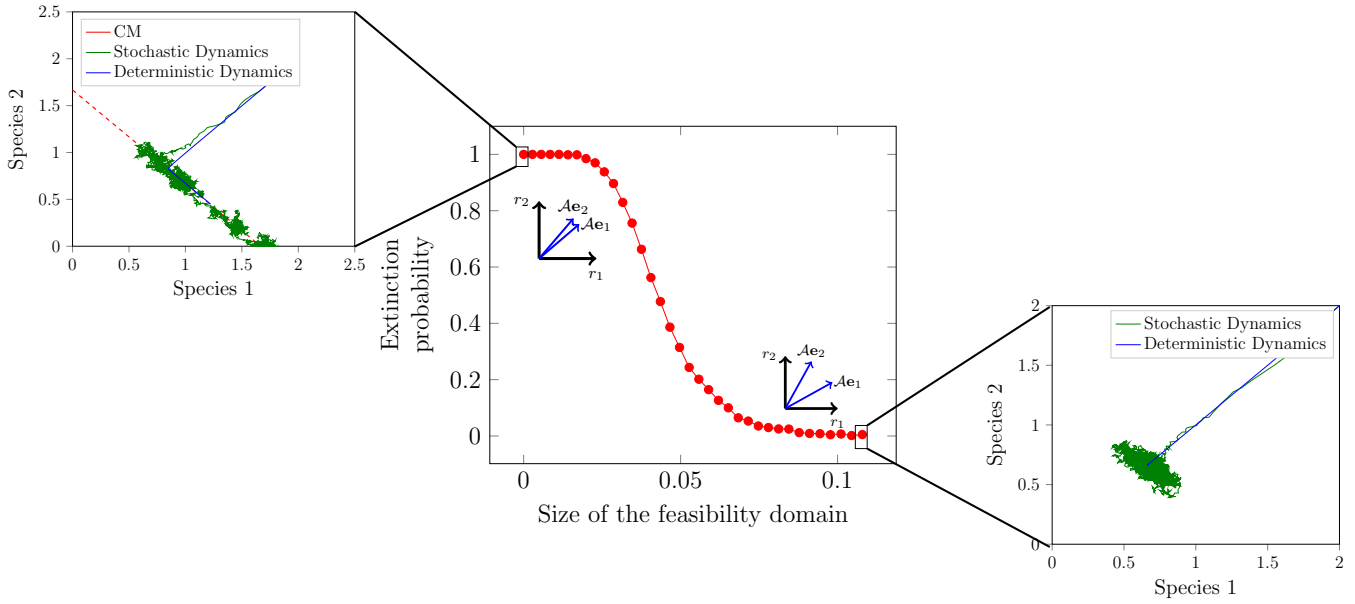


FIG. 4. Extinction probability as a function of the structural stability of the system. The figure shows the fraction of stochastic extinctions in a two species LV system, that is predicted to be feasible in the deterministic setting, as a function of the size of the feasibility domain. We observe a transition from a state in which the probability of extinction is effectively 1 (i.e., the structural approach fails) to a region where this probability is approximately 0 (i.e., validity of the structural approach). The structural stability of the feasible solution increases with the size of the feasibility domain, reducing the effect of stochasticity on feasibility. We run simulations for a time $\tilde{T} \ll T_{\text{ext}} \sim e^N$, where eventually all finite systems will go extinct.

the Jacobian matrix is zero [34]. That is, the feasibility domain shrinks to a line. Then, because stochastic fluctuations of the state variables in the vicinity of the fixed point are equivalent to fluctuations of the parameters [35], infinitesimally small demographic noise can turn feasible into unfeasible solutions. As discussed above, within this regime of parameters (i.e., near neutrality) $T_{\text{ext}} \sim N^\alpha$, extinction takes place with probability 1 in finite time. Note that globally stable fixed points correspond to the opposite side of the spectrum, for which $T_{\text{ext}} \sim e^N$. Thus, focusing on a finite time scale, by moving from one side of the

spectrum to the opposite we can observe an abrupt transition for the extinction probability in times that are small compared to e^N (see Fig. 4). Notably, this probability is a function of the dominant eigenvalue of the Jacobian, and therefore, of the size of the feasibility domain.

The statement above has an important implication for the structure of the feasibility domain itself. In fact, the investigation of the explicit stochastic dynamics reveal that, within the feasibility domain, there exists a nonuniform distribution of the extinction probability. This was already

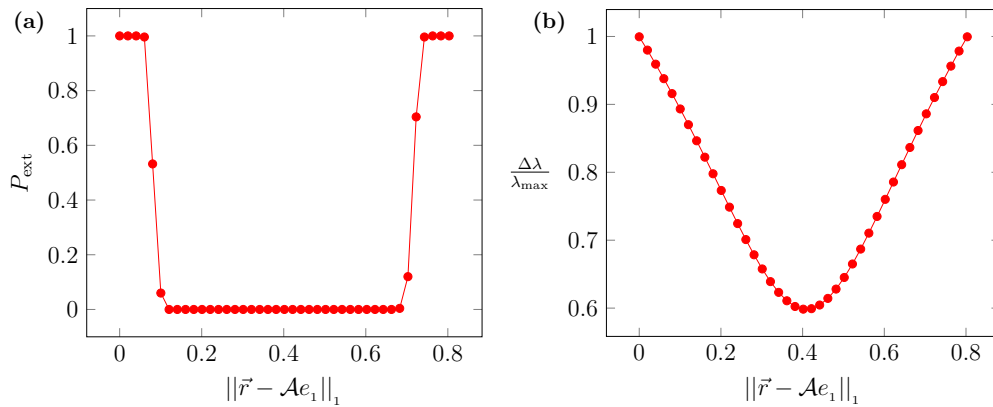


FIG. 5. Partition of a two species feasibility domain in regions that undergo extinctions within different time scales. Panel (a) shows the extinction probability as a function of the position of a vector of intrinsic growth rates inside the feasibility domain. To generate panel (a), we selected a vector of intrinsic growth rates \vec{r} on one of the columns of the feasibility domain and compute the extinction probability of Eq. (11) over an ensemble of 10^3 realizations. Then, we selected a new vector \vec{r} until we reached the opposite border. The x axis shows the distance (in the L_1 norm) of the new sampled vector \vec{r} from the border of the feasibility domain, which we have fixed as origin. Panel (b) shows how the separation of time scales $\Delta\tau$ changes as a function of space on the surface of a two dimensional feasibility domain (i.e., a line).

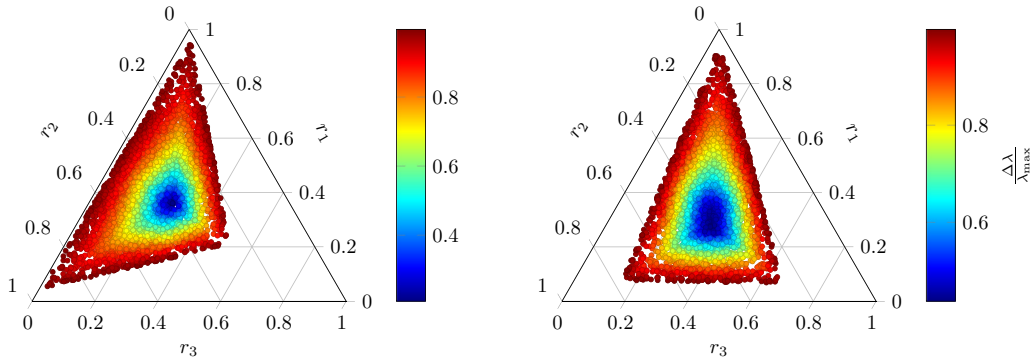


FIG. 6. Structural approach applied to stochastic Lotka-Volterra dynamics. The figure shows the surface of two different feasibility domains in the parameter space of intrinsic growth rates r_i of three-dimensional systems. The colors within the feasibility domains show the relative difference between the largest and smallest eigenvalue of the corresponding Jacobian matrix. Note that the separation of time scales between the most and least stable direction is proportional to the extinction probability. Then, the structural approach can be applied by measuring the size of the region with minimum time-scale separation (center blue region).

noticed in previous work [36] in the context of environmental stochasticity. Importantly, for a given (fixed) population size N and a given (fixed) interaction matrix \mathcal{A} , the distribution of the extinction probability is nonhomogeneous in space (in the parameter space of intrinsic growth rates). As shown in Fig. 5(a), regions near the border of the feasibility domain have a larger extinction probability than regions that are far away from the border. Therefore, using the size of the feasibility domain to study the structural stability of stochastic systems can be misleading. Instead, one needs to use the size of the region within the feasibility domain for which, in finite times, $P_{\text{ext}} = 0$. Note that other regions are deterministically feasible, but will undergo extinction with probability 1 in the presence of demographic noise.

While measuring the extinction probability as a function of the parameter space of high-dimensional feasibility domains is a challenging task, we propose that this can be estimated by the difference between the largest and the smallest eigenvalue of the Jacobian matrix of the deterministic system [see Fig. 5(b)] [37]. Indeed, the lack of structural stability is characterized by a strong separation of time scales between the most stable (largest eigenvalue λ_{max}) and the least stable (smallest eigenvalue λ_{min}) dynamics. Importantly, this separation reaches its minimum within the interior of the feasibility domain, where the slow and fast dynamics are not fully separated. On the contrary, along the borders of the feasibility domain, this separation will be maximum (see Fig. 6). Thus, we can quantify the structural stability of a community by measuring the size of the region, within a feasibility domain, in which the fast and slow dynamics are not well separated. For example, a possible way to perform this analysis is to measure the relative difference of time scales $\Delta\tau = \frac{\lambda_{\text{max}} - \lambda_{\text{min}}}{\lambda_{\text{max}}}$ across the feasible region of the parameter space (see Fig. 6). Then, we can fix a threshold ϵ on $\Delta\tau$ (typically $\epsilon = \Delta\tau_c$ at which P_{ext} goes from 0 to 1) and measure the size of the feasibility domain that falls below this threshold. Generally, the larger this region is, the larger the structural stability of a SLV dynamics. Note that, for fixed N and \mathcal{A} , $\Delta\tau$ is a function of the location of a system in the feasibility domain (i.e., a function of \vec{r}), and resembles the distribution of the extinction probability (see Fig. 5).

V. CONCLUSION

The structural stability of a population dynamics model can be used as a measure to quantify the tolerance of biological communities to environmental perturbations [2]. For example, the structural approach based on the classic LV model uses the size of the feasibility domain (the set of parameter values that guarantees the existence of a fixed point at which all species coexist) as a measure for structural stability [14]. Although this approach was derived to investigate the structural stability of the LV dynamics, its applicability is not limited exclusively to population dynamics models with linear functional responses [15]. Indeed, in this paper, we have shown that the structural approach can be applied to investigate the structural stability of biological communities governed by a large class of deterministic nonlinear models. Furthermore, we have shown how to extend this approach to stochastic models.

In particular, we have shown that in order to guarantee the validity of the structural approach under a general nonlinear model, the functional response of Eq. (3) needs to satisfy Eq. (6). Importantly, these conditions are satisfied by many functional responses that have been found to reasonably explain experimental data [38]. The results of Sec. III imply that the structural approach can be applied even when the underlying population dynamics model changes across time, provided that every model satisfies Eq. (6). This is relevant for the analysis of empirical data. In fact, because the functional response of biological communities are typically context dependent [39], it is advantageous to have methods that do not rely too strictly on the assumption of a particular functional form.

Finally, we have discussed the applicability of the structural approach to investigate the structural stability of the feasible fixed point for populations governed by the SLV dynamics. We have shown that in finite populations, structural stability is strongly correlated with the time-scale separation between fast and slow dynamics. Thus, it is possible to divide regions of the feasibility domain into those where the population exhibits either a zero or nonzero extinction probability in finite times. We have proposed that the size of the region for which the extinction probability is zero can be used as an appropriate

measure of structural stability in finite populations. Note that because the SLV dynamics are derived from a linear noise approximation of a master equation, the extension of the structural approach to Eq. (11) applies to finite but small noise. This should not be seen as a strong limitation of this approach. Empirical studies have shown that stochastic effects are not always the main drivers of community dynamics [40]. Indeed, recent experiments have shown that population dynamics, in closed communities, exhibit a strong deterministic component with stochasticity mainly driven by environmental variations [41]. Overall, we hope that this research will serve as a baseline for future studies investigating the structural stability

of biological communities, where the dynamics are typically driven by time-varying, nonlinear, functional responses and by small demographic stochasticity [42].

ACKNOWLEDGMENTS

We would like to thank R. P. Rohr and C. Song for insightful discussions. Funding was provided by the MIT Research Committee Funds and the Mitsui Chair (S.S.).

S.C. and S.S. designed the study, S.C. performed the study, and S.S. supervised the study. S.C. and S.S. wrote the paper.

-
- [1] R. Levins, *Evolution in Changing Environments: Some Theoretical Explorations* (Princeton University Press, Princeton, NJ, 1968).
- [2] R. Thom and D. Fowler, *Structural Stability and Morphogenesis: An Outline of a General Theory of Models*, The Advanced Book Program (W. A. Benjamin, New York, 1975).
- [3] H. Ye, R. J. Beamish, S. M. Glaser, S. C. Grant, C.-H. Hsieh, L. J. Richards, J. T. Schnute, and G. Sugihara, *Proc. Natl. Acad. Sci. USA* **112**, E1569 (2015).
- [4] J. H. Vandermeer, *Ecology* **50**, 362 (1969).
- [5] D. Logofet, *Matrices and Graphs: Stability Problems in Mathematical Ecology* (CRC, Boca Raton, 1993).
- [6] D. Tilman, *Am. Nat.* **129**, 769 (1987).
- [7] A. J. Lotka, *Proc. Natl. Acad. Sci.* **6**, 410 (1920).
- [8] V. Volterra and M. Brelot, *Leçons sur la Théorie Mathématique de la Lutte pour la Vie*, Cahiers Scientifiques (Gauthier-Villars, Paris, 1931).
- [9] K. Michaelian, *J. Theor. Biol.* **237**, 323 (2005).
- [10] U. C. Täuber, *J. Phys.: Conf. Ser.* **319**, 012019 (2011).
- [11] J. A. Vano, J. C. Wildenberg, M. B. Anderson, J. K. Noel, and J. C. Sprott, *Nonlinearity* **19**, 2391 (2006).
- [12] J. Hofbauer and J.-H. So, *Appl. Math. Lett.* **7**, 65 (1994).
- [13] R. C. Lewontin, *Brookhaven Symp. Biol.* **22**, 13 (1969).
- [14] R. P. Rohr, S. Saavedra, and J. Bascompte, *Science* **345**, 1253497 (2014).
- [15] S. Saavedra, R. P. Rohr, J. Bascompte, O. Godoy, N. J. B. Kraft, and J. M. Levine, *Ecol. Monogr.* **87**, 470 (2017).
- [16] S. Saavedra, R. P. Rohr, J. M. Olesen, and J. Bascompte, *Ecol. Evol.* **6**, 997 (2016).
- [17] S. Saavedra, S. Cenci, E. del Val, K. Boege, and R. P. Rohr, *J. Anim. Ecol.* **86**, 1136 (2017).
- [18] C. Song, R. P. Rohr, and S. Saavedra, *J. Anim. Ecol.* **86**, 1417 (2017).
- [19] S. Saavedra, R. P. Rohr, L. J. Gilarranz, and J. Bascompte, *J. R. Soc. Interface* **11**, 20140693 (2014).
- [20] G. W. A. Constable and A. J. McKane, *Phys. Rev. Lett.* **114**, 038101 (2015).
- [21] G. W. A. Constable and A. J. McKane, *Phys. Rev. E* **96**, 022416 (2017).
- [22] C. Mayo-Wilson, *Philos. Sci.* **82**, 1236 (2015).
- [23] J. Hofbauer and K. Sigmund, *The Theory of Evolution and Dynamical Systems: Mathematical Aspects of Selection*, London Mathematical Society student texts (Cambridge University Press, Cambridge, 1988) translation of *Evolutions Theorie und Dynamische System*.
- [24] S. Kauffman, *The Origins of Order: Self-organization and Selection in Evolution* (Oxford University Press, Oxford, 1993).
- [25] S. Cenci, A. Montero-Castaño, and S. Saavedra, *J. Theor. Biol.* **437**, 115 (2018).
- [26] Y. Takeuchi, *Global Dynamical Properties of Lotka-Volterra Systems* (World Scientific, Singapore, 1996).
- [27] N. van Kampen, *Stochastic Processes in Physics and Chemistry*, North-Holland Personal Library (Elsevier Science, Amsterdam, 1992).
- [28] C. W. Gardiner, *Handbook of Stochastic Methods for Physics, Chemistry and the Natural Sciences*, 3rd ed., Springer Series in Synergetics Vol. 13 (Springer-Verlag, Berlin, 2004).
- [29] A. J. McKane, T. Biancalani, and T. Rogers, *Bull. Math. Biol.* **76**, 895 (2014).
- [30] S. Rulands, A. Zielinski, and E. Frey, *Phys. Rev. E* **87**, 052710 (2013).
- [31] A. Dobrinevski and E. Frey, *Phys. Rev. E* **85**, 051903 (2012).
- [32] G. W. A. Constable, T. Rogers, A. J. McKane, and C. E. Tarnita, *Proc. Natl. Acad. Sci.* **113**, E4745 (2016).
- [33] J. Cremer, T. Reichenbach, and E. Frey, *New J. Phys.* **11**, 093029 (2009).
- [34] J. Duan, *An Introduction to Stochastic Dynamics*, Cambridge Texts in Applied Mathematics (Cambridge University Press, Cambridge, England, 2015).
- [35] J.-F. Arnoldi, M. Loreau, and B. Haegeman, *J. Theor. Biol.* **389**, 47 (2016).
- [36] R. P. Rohr, S. Saavedra, G. Peralta, C. M. Frost, L.-F. Bersier, J. Bascompte, and J. M. Tylianakis, *Am. Nat.* **188**, 411 (2016).
- [37] T. L. Parsons and T. Rogers, *J. Phys. A: Math. Theor.* **50**, 415601 (2017).
- [38] F. J. Ayala, M. E. Gilpin, and J. G. Ehrenfeld, *Theor. Popul. Biol.* **4**, 331 (1973).
- [39] J. T. A. Dick, M. E. Alexander, A. Ricciardi, C. Laverty, P. O. Downey, M. Xu, J. M. Jeschke, W.-C. Saul, M. P. Hill, R. Wasserman, D. Barrios-O'Neill, O. L. F. Weyl, and R. H. Shaw, *Biol. Invasions* **19**, 1667 (2017).
- [40] J. C. Stegen, X. Lin, A. E. Konopka, and J. K. Fredrickson, *ISME J.* **6**, 1653 (2012).
- [41] Z. Frenzt, S. Kuehn, and S. Leibler, *Phys. Rev. X* **5**, 041014 (2015).
- [42] The code for reproducing the figures will be available on GitHub at <https://github.com/MITEcology/Phys-Rev-E-Cenci-et-al-2017>.