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AN OPEN-SYSTEM APPROACH TO COMPLEX BIOLOGICAL NETWORKS*

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Abstract. Biological diversity is essential for the maintenance of the ecosystem functions that support life on the planet. Inherent to this diversity is the seemingly endless way in which the biological entities of a natural system interact and affect each other at local and regional scales, conforming complex ecological networks permeable to external forcing. Existing approaches to capture and model such complexity typically make unrealistic or excessively restrictive assumptions. Here we use concepts from open dynamical systems and metacommunity theory to develop a framework in which the system dynamics is a function of both interspecific interactions in the focal system (e.g., a local community of coexisting species) and unobserved biotic and abiotic interactions with the local and regional environment (e.g., the metacommunity). Species in the focal system interact through direct exchanges of biomass (i.e., trophic interactions), as well as through altering the acquisition and/or transformation of biomass by other species (nontrophic interactions). Interactions are affected by environmental fluctuations and by migration and emigration processes, which can take place at different time scales and can be modeled by stochastic differential equations driven by a mixture of continuous and discontinuous processes. In this manner, the proposed framework provides a wider and more flexible representation of the complexity of ecological systems, in comparison with the closed-system paradigm that isolates the system from the environment. Because the core model explicitly recognizes the existence of local and regional processes, it is also a natural starting point to examine spatially structured networks.

Key words. open-system dynamics, Lévy processes, ecological networks

AMS subject classifications. 92D40, 60H30

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1. Introduction.

Living entities are open systems in continuous interaction with their surrounding environment [1]. They form spatio-temporal ensembles of interacting individuals, which can be represented as a network whose components are engaged in the transfer of matter, energy, and information. Ecologists have tried to

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understand the structure and dynamics of these complex networks and, for practical purposes, have defined arbitrary, spatially delimited local ecological communities as units of study. It is nonetheless broadly recognized that ecological systems are open, in the same way as populations and communities are—constantly exchanging matter and energy with their surrounding environment, and with the larger region in which they are embedded.

Interestingly, ever since Lotka and Volterra's foundational papers in the 1920s [2, 3, 4, 5], local ecological communities have been largely modeled as closed systems undergoing deterministic dynamics, where a few species are engaged with each other in a given type of interaction (e.g., competition or predation). Such systems have well-defined equilibria and stability properties (e.g., [6]), which facilitates their study and provides results that have often given rise to paradigmatic lines of theoretical and empirical research (e.g., diversity-stability debate, predator-prey cycles, alternative stable states). In this framework, however, the environment has seldom been taken into account, even though, as May [6] recognized, real environments are uncertain and stochastic. Therefore, the question is not whether the environment is invariant, but "When do deterministic models say sensible things about the environmentally stochastic reality, and when do they not?" [6]. The approach to answering this question has traditionally been to include the fluctuating environment as another deterministic component or as an added noise affecting the growth rate or carrying capacity of populations [6, 7, 8]. Our approach here goes beyond that and uses stochastic processes to model open-system dynamics. That is, *we claim that open-system theory plays a foundational role in stochastic modeling* and that this framework is oftentimes better suited to represent ecological dynamics. This is supported by a number of well-known theoretical advances. Let us mention, for instance, the mathematical construction of Brownian motion developed within the framework of classical (or Kolmogorov) probability theory, or in physics, the study of open quantum systems, based on noncommutative probabilities (see [16, 32, 33]). Furthermore, much of modern finance is now modeled through stochastic differential equations. In all of these examples, the dynamics appears as a complex interplay between the observed main system and its unobserved environment driven by noise. Thus, probabilities and stochastic processes—in commutative and noncommutative versions—appear as the adequate mathematical concepts to deal with open systems, including species in ecological networks.

Moreover, the importance of including different interaction types has been amply recognized since May's influential paper [9] in 1972, but this has long been considered a hopeless exercise given the complexity of ecological communities [7]. Only recently have conceptual advances suggested ways in which combinations of interactions (trophic and non-trophic, positive and negative) can be included in models using sets of deterministic biomass transformation equations [10, 11, 13]. These pioneering conceptual and mathematical propositions have shown a path for more theoretical work, but are nonetheless still based on the deterministic closed-system paradigm.

In sum, current ecological models typically do not take into account that all local ecological systems are embedded in an environment that not only contains various interaction types that simultaneously link a given set of species, but is also subject to stochastic fluctuations in biotic and abiotic conditions that alter birth, death, and immigration processes of all species, locally and regionally. Furthermore, the question of different spatial and temporal scales becomes crucial when going beyond trophic interactions to consider the whole web of interactions taking place in a local ecological community. Indeed, non-trophic interactions (e.g., mutualistic and competitive) and

dispersal processes can occur at a different temporal scale than that of trophic ones.

The concepts of a *local system* and its *environment* used to define ecological systems have their correspondence in the *main system* and *reservoir* (or *environment*) of open dynamical system theory, which has been mostly developed for open quantum systems [16]. In this contribution, we build upon this analogy and the premise that, like any natural phenomenon, ecological objects cannot be isolated from their own motion. In other words, the dynamics of ecological communities is of the open type, and the observed (or main) system is continuously evolving, always exchanging matter, energy, and information with its environment, which represents multiple unobserved interactions. We define a local community as a well-observed set of species living and interacting in a local area, and subjected to stochastically varying environmental conditions and biotic interactions with the same or other species living outside the focal community (i.e., at regional or metacommunity scales). These interactions (with the environment as well as with other species), and other relevant processes that may affect the dynamics of the main system or community, occur at different time scales from very slow or infrequent (e.g., large disturbances, speciation) to very frequent ones (e.g., competition, predation), which accounts for the complexity of how to model these different time scales. In a stochastic framework the interaction between the main system and the environment is usually modeled as a white noise or Brownian process [6, 7, 14, 15] which represents a single time scale. One way of representing more than one time scale is by considering Lévy-type processes which combine fast-scale continuous perturbations and slow discontinuous ones. In summary, we propose a general stochastic model for biological networks that can accommodate positive-, negative-, and neutral-type interactions and more than one time scale.

2. Constructing the model. We use the term *state-of-the-system* to denote the biomass probability distribution of different species within the local community. This marks a departure from the traditional usage of system state in closed systems (e.g [17]). Thus, our *main system* is defined by our observed quantities, which are functions of the biomass. Usually, the proportion of individuals of a given species, inside a population of size N, defines its *relative abundance*. If the number N of individuals of all species grows indefinitely, that proportion eventually gives the probability distribution of that species (law of large numbers). That is, the biomass probability distribution of each species—our states—coincides with its *relative abundance* under the neutral assumption that all individuals are equal [18].

We consider a main system of d-species—also called the *focal system*—defining a graph or network G. Each node i of the graph is a species. Let us denote by $x_i \in [0,1]$ the proportion of biomass with respect to the carrying capacity of the species i, so that a vector

$$x = \begin{pmatrix} x_1 \\ \vdots \\ x_d \end{pmatrix} \in E = [0,1]^d$$

represents the collection of species biomass proportions in the focal system.

2.1. The flow of biomass proportions. Following the custom in probability theory, we use small letters x, x_i to denote the values attained by stochastic processes, which are denoted by capital letters $X(\omega,t)$, $X_i(\omega,t)$. To alleviate writing, we drop the ω, which is always implicit, keeping the variable t only, as in $X(t)$, $X_i(t)$. Our open-system approach considers the evolution of the biomass via the stochastic process $X(t)$, with components $X_i(t)$, $i = 1,\ldots,d$, the biomass proportion of each species i

$(0 \leq X_i(t) \leq 1)$ or its random relative abundance (RRA). The mean value $\mathbb{E}(X_i(t))$ corresponds to the mean relative abundance (MRA) of the species i at time t, while the probability distribution of $X_i(t)$ corresponds to its relative abundance. Thus, the probability distribution P_t of the vector random process $X(t)$ represents the relative abundance of the whole focal community at time t. This probability characterizes the *state* of the system at a given time. Its evolution is determined by the dynamics of the flow of biomass, represented by the process $X(t)$, given in the form of stochastic differential equations, depending on the biomass transfer functions between species.

2.2. Transfer functions. The transfer functions $\alpha_{i,j}$ from node (or species) i towards the node j $(i \to j)$ are given in the form

$$\alpha_{i,j}(x) = a_{i,j}(x)x_i \quad (x \in E;\ i,j = 1,\dots,d). \tag{1}$$

Hypothesis 1. We assume that the transfer $i \to j$ depends linearly on the biomass of the species i, but the rate $a_{i,j}(x)$ depends on the whole focal system biomass. In this case, we assume that each function $a_{i,j}(x)$ is continuously differentiable and

$$\sup_{1\leq i,j\leq d} \sup_{x\in E} |\alpha_{i,j}(x)| < 1,$$

for technical reasons. Typically, these coefficients will represent functional responses or birth and death rates. Throughout this paper, we assume the form (1) for the family of functions $\alpha_{i,j}(x)$. We call $A(x)$ the $d \times d$ matrix of all the $a_{i,j}(x)$'s and $\mathrm{diag}(A(x))$ its diagonal, which contains the net change of biomass per unit time in isolation, without interacting with other species. Notice that the bound assumed on the coefficients $a_{i,j}(x)$ leads to $\sup_{x\in E} \|A(x)\| < \sqrt{d}$, where $\|\cdot\|$ denotes the norm of $d \times d$ matrices. Finally, let us call $A_0(x) = A(x) - \mathrm{diag}(A(x))$ the matrix with 0's on the diagonal, and denote its components as $a^0_{i,j}(x) = (1-\delta_{i,j})a_{i,j}(x)$, $i,j = 1,\dots,d$.

2.3. The interaction with the environment: Fast and slow time scales. No ecological network will take into account all species in a given focal system or community, including viruses, bacteria, and other microorganisms as well as macroscopic multicellular ones. Thus, unobserved or omitted species are also part of the environment or "reservoir" that includes fluctuations in the abiotic environment, and cannot be dismissed. They interact, changing the transfer functions on the graph. Indeed, these transfer functions become $\alpha_{i,j}(X_t(\omega))$ when evaluated on the total focal system biomass at time t, and $X_t(\omega)$ is random since its evolution is given by a stochastic differential equation. Moreover, this stochastic evolution includes two different time scales for interactions with the environment: a fast one driven by a continuous process and a slower discontinuous one, associated, for instance, to immigration or emigration pulses or to extreme climatic events.

Hypothesis 2. Given a quantity $x = (x_1,\dots,x_d) \in E$ of biomass proportion, we denote $\sigma(x)$ the vector with components $\sigma_i(x) = \sqrt{\gamma_i x_i(1-x_i)}$, the rate of fluctuations of biomass of species i due to changes of the whole biomass of the system, or due to temperature or other fluctuations in the environment. We assume $0 < \gamma_i < 1$ for all $i = 1,\dots,d$. Thus, $0 \leq \sigma_i(x) < 1/2$.

To include discontinuous perturbations, we first denote m the vector with components $0 \leq m_i < 1$ representing the mean rate of migration of each species, and we call $\eta(x)$ the vector with components $\eta_i(x) = m_i x_i$, which is the instantaneous migrated biomass of the species i.

Hypothesis 3. Correspondingly, two kinds of *noises* may be used to model the interactions with the environment: a Brownian motion W for the faster time scale

and a compound Poisson process Z for the second. They characterize a Lévy type of stochastic differential equation [19]. To write differential equations with respect to discontinuous noises like Z one needs to take care of jumps of trajectories. Below, for instance, we denote $X(t-)$ the left-hand limit of X at time t, that is, $X(t-) = \lim_{s<t,\, s\to t} X(s)$.

2.4. Evolution of the biomass flow. According to our previous hypotheses and notation, the biomass evolution within the network is described by the following stochastic differential equation:

$$\left\{\begin{array}{rcl} dX_i(t) & = & \left(\displaystyle\sum_{j=1, j\neq i}^{d} \alpha_{j,i}(X(t))X_i(t) - \sum_{j=1}^{d} \alpha_{i,j}(X(t))X_j(t)\right) dt \\ & & + \sigma_i(X(t))dW(t) + \eta_i(X(t-))dZ_i(t), \quad (i = 1, \ldots, d), \\ X_i(0) & = & x_i, \end{array}\right. \tag{2}$$

where the column vector x with coordinates $x_i \in [0, 1]$ is the initial data, the process W is a Brownian motion, and Z is an independent compound Poisson process defined as follows. We denote N a canonical Poisson process, we consider an independent sequence $(\xi_{i,n})_{i,n}$ $(1 \leq i \leq d;\ n \in \mathbb{N})$ of identically distributed Bernoulli random variables with values ± 1, and we call $p_i = \mathbb{P}(\xi_{i,n} = 1)$, $q_i = 1 - p_i$. The process Z is then defined as

$$Z_i(t) = \sum_{k=1}^{N(t)} \xi_{i,k}, \qquad Z(t) = \begin{pmatrix} Z_1(t) \\ \vdots \\ Z_d(t) \end{pmatrix}. \tag{3}$$

Notice that the mean value of each $Z_i(t)$ is $\mathbb{E}\left(Z_i(t)\right) = (p_i - q_i)t = (2p_i - 1)t$. Given two vectors $x, y \in \mathbb{R}^d$, we denote $x \bullet y$ the Schur product of these vectors, which is the vector with components $x_i y_i$. Notice that this product is commutative in $\mathbb{R}^d$. So, the previous equation becomes in vector notation

$$\left\{\begin{array}{rcl} dX(t) & = & X(t) \bullet \left([A_0^T(X(t)) - A(X(t))]X(t)\right) dt \\ & & + \sigma(X(t))dW(t) + \eta(X(t-)) \bullet dZ(t), \\ X(0) & = & x. \end{array}\right. \tag{4}$$

Equivalently, in integral form,

$$\begin{array}{rcl} X(t) & = & x + \displaystyle\int_0^t X(s) \bullet \left([A_0^T(X(s)) - A(X(s))]X(s)\right) ds \\ & & + \displaystyle\int_0^t \sigma(X(s))dW(s) + \int_0^t \eta(X(s-)) \bullet dZ(s). \end{array} \tag{5}$$

To summarize, the previous equations rule the dynamics of different species biomass $X_i(t)$, taking into account their mutual relations determined by the transfer functions $\alpha_{i,j}$. In addition, one obtains a description of the evolution of the whole focal system biomass through the vector process $X(t)$, given an initial value $X(0) = x \in E$. This is the *flow of biomass*.

2.5. The evolution of observables. Moreover, any observation of that system is given as a function $f(X(t))$, and a measurement is a mean value of it. In particular, the function $t \mapsto f(t, x) = \mathbb{E}\left(f(X(t))|X(0) = x\right)$, the mean value of $f(X(t))$

conditioned to the initial biomass $X(0) = x$, provides the evolution of the observation implemented with f. And the probability distribution of the process $X(t)$ (characterized by its density $\rho_t(x)$) represents the abundance of species in the focal system at time t. So, it becomes crucial to prove that there is a solution to (4) (or, equivalently, (5)). Theorem 1 below is the main theoretical result characterizing the existence of solutions to the previous system of equations. In addition, the flow of biomass $X(t)$ is a Markov process, and as a by-product one obtains the equations of Chapman and Kolmogorov (respectively, Fokker and Planck) characterizing the evolution of both the observations $f(t,x)$ and the abundances $\rho_t(x)$.

3. Existence and uniqueness of the biomass flow and its mathematical properties. As a first remark, notice that (5) makes sense for a stochastic process X with values in $\mathbb{R}^d$ under the condition $\mathbb{P}(X(t) \in E) = 1$. This is obvious, since one needs the coefficient $\sigma(X(t))$ to be a positive number and, moreover, the process corresponds to a vector of random proportions of species. Equations like (5) have been solved under Lipschitz-type conditions on the coefficients. In our case, $\sigma(x)$ is not Lipschitz and that requires us to approach the distribution of the solution by a sequence of probabilities $(\mathbb{P}_N)_{N\geq 1}$ solving (5) for regularized coefficients $(\sigma^{(N)}(x))_{N\geq 1}$ that converge uniformly to $\sigma(x)$ for any x in the compact set E.

3.1. Solving (5) in distribution.

THEOREM 1. *There exist a probability space* $(\Omega, \mathcal{F}, \mathbb{P})$ *and a stochastic process* $(X(\omega,t))_{t\geq 0}$ *defined therein,* $X(\omega,t) \in E$ *almost surely for all* $t \geq 0$*, which is a unique solution in distribution to the stochastic differential equation* (4)*, given* $X(\omega,0) = x \in E$*.*

Proof. The basic probability space is built up as follows. Call $E = [0,1]^d$, and $\overset{o}{E}$ the interior of the compact set E. Consider the set of all E-valued functions defined on $\mathbb{R}^+$, which are right-continuous with left-hand limits on every point of $\mathbb{R}^+$ (the so-called *cadlag* functions). Call this set Ω, endowed with the Skorokhod topology, so that each $\omega \in \Omega$ is a function $\omega = (\omega(t),\ t \geq 0)$, where $\omega(t) \in \mathbb{R}^d$. Let us define the so-called *canonical process* as $X(t,\omega) = \omega(t)$ $(t \geq 0)$.

We define the increasing family of σ-fields $\mathcal{F}_t$ as $\bigcap_{s>t} \sigma(X(u),\ u \leq s)$, and $\mathcal{F} = \mathcal{F}_\infty = \sigma(X_t,\ t \geq 0)$. Furthermore, let us define the stopping time:

$$\tau_E(\omega) := \inf\left\{t \geq 0 :\ X(t,\omega) \notin \overset{o}{E}\right\} \quad (\inf \emptyset = \infty). \tag{6}$$

As usual, to prove Theorem 1, a probability $\mathbb{P}$ is constructed on the measurable space $(\Omega, \mathcal{F})$, such that $\mathbb{P}(\tau_E < \infty) = 1$, so that the stopped process $X^{\tau_E} = X$ almost surely, and the process X satisfies the integral version of equation (4), that is, (5), $\mathbb{P}$-a.s.

So, the proof has two parts. First, we work with a sequence of C^∞ functions $(\sigma_N)_{N\in\mathbb{N}}$ of coefficients which approach σ, obtaining a sequence of probabilities $(\mathbb{P}_N)_{N\in\mathbb{N}}$ on Ω. The second part shows the convergence of $\mathbb{P}_N$ to a limit $\mathbb{P}$ which provides the solution to the original equation.

Construction of the probability $\mathbb{P}_N$. For any bounded measurable function f defined on $[0,1]$ and $N \in \mathbb{N}$, let us define

$$B_N f(x) = \sum_{k=0}^{N} \binom{N}{k} f\left(\frac{k}{N}\right) x^k (1-x)^{N-k}.$$

Then we consider the vector function

$$\sigma^{(N)}(x) = \begin{pmatrix} B_N\sigma_1(x_1) \\ \vdots \\ B_N\sigma_d(x_d) \end{pmatrix} \quad (x \in E).$$

Therefore, each $\sigma^{(N)}$ has bounded derivatives in E and the sequence converges uniformly to the continuous function σ.

Now, we construct below the probability $\mathbb{P}_N$ as the distribution of the solution to the equation

$$\begin{aligned} X(t) &= X(0) + \int_0^t X(s) \bullet \left([A_0^T(X(s)) - A(X(s))]X(s)\right) ds \\ &\quad + \int_0^t \sigma^{(N)}(X(s))dW(s) + \int_0^t \eta(X(s-)) \bullet dZ(s). \end{aligned} \tag{7}$$

This follows as a straightforward application of Theorem 6.2.3 in [19, p. 367]. To this end, we check the hypotheses of that theorem. These conditions are the *Lipschitz condition* (C1) and the *growth condition* (C2). Call $M(t) = Z(t) - (p-q)t$, where p (respectively, q) is the vector with p_i (respectively, q_i) components, $t \geq 0$. M is a martingale with zero mean.

Verification of (C1). Denote $|\cdot|$ the Euclidean norm of vectors in $\mathbb{R}^d$ and $\|\cdot\|$ the norm of matrices. Call $F(x) = (A_0^T(x) - A(x))x$. This is a continuous differentiable function, and due to our hypotheses, $\sup_{x\in E} \|F(x)\| < 2d^{1/2}$. Consider

$$b(x) = x \bullet (A_0^T(x) - A(x))x = x \bullet F(x). \tag{8}$$

The functions $\sigma^{(N)}$ and F have continuous differentials $D\sigma^{(N)}(x)$, $DF(x)$ for all x at the interior of E. In addition, for all $x \in E$, $\left|\sigma^{(N)}(x)\right| \leq |\sigma(x)| \leq \frac{d^{1/2}}{2}$. Define

$$L = \sup_{x\in E} \left\{ \left\| D\sigma^{(N)}(x) \right\|, \|DF(x)\| \right\}, \qquad K = 2d^{1/2} + \frac{d^{1/2}}{2} + |m|.$$

Thus, for any $x_1, x_2 \in E$,

$$\begin{aligned} |b(x_1) - b(x_2)|^2 &= |x_1 \bullet F(x_1) - x_2 \bullet F(x_2)|^2 \\ &\leq |F(x_1)|^2 |x_1 - x_2|^2 + R^2 |F(x_1) - F(x_2)|^2 \\ &\leq (K^2 + L^2 d) |x_1 - x_2|^2. \end{aligned} \tag{9}$$

In addition,

$$\begin{aligned} |\eta(x_1) - \eta(x_2)|^2 &= |m \bullet x_1 - m \bullet x_2|^2 \\ &\leq K^2 |x_1 - x_2|^2. \end{aligned} \tag{10}$$

$$\left|\sigma^{(N)}(x_1) - \sigma^{(N)}(x_2)\right|^2 \leq L^2 |x_1 - x_2|^2. \tag{11}$$

Verification of (C2). In our case, we easily obtain

$$|b(x)|^2 + \left|\sigma^{(N)}(x)\right|^2 + |\eta(x)|^2 \leq \left(2K^2 + L^2\right)\left(1 + |x|^2\right) \text{ for all } x \in E. \tag{12}$$

The expressions (9), (10), (11), and (12) guarantee the existence and uniqueness of a strong solution to (7) according to Theorem 6.2.3 in [19], for each fixed $N \geq 1$. This strong solution is constructed as the limit of a Picard-type sequence of processes $(Y_m)_m$ as follows. Let $x \in \overset{o}{E}$ and define, for all $t \geq 0$, $Y_0(t) = x$, so that $Y_0^{\tau_E} = x = Y_0$. Assume $Y_0, \ldots, Y_m$ constructed such that $Y_k^{\tau_E} = Y_k$ for $k = 0, \ldots, m$. Then define

$$\begin{aligned} Y_{m+1}(t) &= x + \int_0^{t\wedge\tau_E} Y_m(s) \bullet \left([A_0^T(Y_m(s)) - A(Y_m(s))]Y_m(s)\right) ds \\ &\quad + \int_0^{t\wedge\tau_E} \sigma^{(N)}(Y_m(s))dW(s) + \int_0^{t\wedge\tau_E} \eta(Y_m(s-)) \bullet dZ(s). \end{aligned}$$

Thus, as in the proof of Theorem 6.2.3 in [19], under the hypotheses (C1) and (C2), this sequence converges almost surely to a solution Y of the stochastic differential equation which, in addition, satisfies $Y^{\tau_E} = Y$. Call $\mathbb{P}_N$ the probability distribution of this solution. Then, $\mathbb{P}_N(X(t) \in \overset{o}{E}) = 1$.

It is worth noticing for further use that each Y_m as a function of t has right-continuous trajectories with left-hand limits. Moreover, each Y_m as a function of $x \in E$ is measurable.

Solving (5) *in distribution.* We first notice that

$$|\Delta X(t)| \leq |m|, \tag{13}$$

for all $t \geq 0$, and almost surely for each probability $\mathbb{P}_N$. Assume a sequence of uniformly bounded stopping times T_N and positive numbers $\delta_N \downarrow 0$. The following bound holds (mean values taken with respect to the probability $\mathbb{P}_N$):

$$\begin{aligned} \mathbb{E}\left(|X(T_N+\delta_N) - X(T_N)|^2\right) &\leq 3\mathbb{E}\left(\left|\int_{T_N}^{T_N+\delta_N} b(X(s))ds\right|^2\right) \\ &\quad +3\mathbb{E}\left(\left|\int_{T_N}^{T_N+\delta_N} \sigma^{(N)}(X(s))dW(s)\right|^2\right) \\ &\quad +3\mathbb{E}\left(\left|\int_{T_N}^{T_N+\delta_N} \eta(X(s-)) \bullet dZ(s)\right|^2\right) \\ &\leq 3\mathbb{E}\left(\delta_N \int_{T_N}^{T_N+\delta_N} |b(X(s))|^2 ds\right) \\ &\quad +3\mathbb{E}\left(\int_{T_N}^{T_N+\delta_N} \sigma^{(N)}(X(s))^2 ds\right) \\ &\quad +3\max_i |m_i| R\mathbb{E}\left((N(T_N+\delta_N) - N(T_N))^2\right) \\ &\leq 3\delta_N \left(\sup_{x\in E}|b(x)|^2 + \sup_{x\in E}|\sigma(x)|^2 + \max_i |m_i| R(1+\delta_N)\right). \end{aligned}$$

As a result, $\mathbb{E}\left(|X(T_N+\delta_N) - X(T_N)|^2\right) \to 0$ as $N \to \infty$. And by Chebyshev's inequality it follows that

$$\mathbb{P}_N\left(|X(T_N+\delta_N) - X(T_N)| > \epsilon\right) \to 0 \quad \text{as } N \to \infty, \text{ for all } \epsilon > 0. \tag{14}$$

Since $X(0)$ is fixed, (13) and (14) imply that the sequence of probabilities $(\mathbb{P}_N)_{N\in\mathbb{N}}$ is tight, so that there exists a convergent subsequence. If necessary, one can choose a further subsequence to have that $\mathbb{P}_{N(n)}$ converges weakly to a probability $\mathbb{P}$ and $\sigma^{(N(n))}(x)$ converges to $\sigma(x)$ uniformly on $x \in E$.

Consider the processes

$$M^{(N(n))}(t) = \int_0^t \sigma^{(N(n))}(X(s))dW(s) \quad (t \geq 0). \tag{15}$$

This is a continuous martingale under the probability $\mathbb{P}_{N(n)}$. Notice that

$$\begin{aligned} M^{(N(n))}(t) &= X(t) - X(0) - \int_0^t X(s) \bullet \left([A_0^T(X(s)) - A(X(s))]X(s)\right) ds \\ &\quad - \int_0^t \eta(X(s-)) \bullet dZ(s). \end{aligned}$$

In addition, for all $T \geq 0$, it holds that $\sup_{t\in[0,T]} \left|\sigma^{(N(n))\,2}(X(t)) - \sigma^2(X(t))\right| \to 0$ in $\mathbb{P}_{N(n)}$ probability as $n \to \infty$. Applying Proposition III.2.4 in [20], under the limiting probability $\mathbb{P}$, the process

$$M(t) = X(t) - X(0) - \int_0^t X(s) \bullet \left([A_0^T(X(s)) - A(X(s))]X(s)\right) ds - \int_0^t \eta(X(s-)) \bullet dZ(s)$$

is represented as $M(t) = \int_0^t \sigma(X(s))dW(s)$ $(t \geq 0)$, so that X solves (5) under the probability $\mathbb{P}$.

Finally, the uniqueness of $\mathbb{P}$ follows as in [19, p. 372], by means of a Gronwall-type inequality. Thus, as a by-product, one obtains that any convergent subsequence of $\mathbb{P}_N$ converges to the same limit $\mathbb{P}$, and this means that the whole sequence $\mathbb{P}_N$ converges weakly to $\mathbb{P}$ as $N \to \infty$. In addition, under $\mathbb{P}$, the process X is Markov (see, for instance, [21, Chap. XIII]).

Furthermore, for all $t \geq 0$, $1 = \limsup_{N\to\infty} \mathbb{P}_N(X(t) \in E) \leq \mathbb{P}(X(t) \in E)$. ∎

3.2. The Markov semigroup. Given $x \in E$, we denote $\mathbf{P}_x$ the probability distribution of the solution to (5) with the initial value $X(0) = x$. That is, given a set $A \in \mathcal{F}$, its probability under $\mathbf{P}_x$ is $\mathbf{P}_x(A) = \mathbb{P}(A|X(0) = x)$.

As in [19, Thm. 6.4.2], one easily obtains the following corollary, which follows from the properties of the Picard sequence used in the proof of Theorem 1.

COROLLARY 1. *Under the probability $\mathbf{P}_x$, the process X has right-continuous trajectories with left-hand limits almost surely, and moreover, it is a Lévy process for all $x \in E$.*

Let us denote $(T_t)_{t\geq 0}$ the family of applications defined for all bounded Borel functions $f : E \to \mathbb{R}$ by

$$T_t f(x) = \mathbb{E}\left(f(X(t))|X(0) = x\right) = \mathbf{E}_x\left(f(X(t))\right) \quad (t \geq 0, x \in E). \tag{16}$$

Given $x \in E$, we consider the operation which consists in modifying its ith coordinate by migrations (c^+ corresponds to immigrations, and c^- to emigrations): for each $i = 1, \ldots, d$, define $c_i^{\pm}(x) = y$, where y is the vector with components

$$y_j = \begin{cases} x_j & \text{if } j \neq i, \\ 0 \vee x_i(1 \pm m_i) \wedge 1 & \text{if } j = i. \end{cases} \tag{17}$$

The above notation allows us to write *jump operators* $D^{\pm}$ for all bounded Borel functions defined on E as follows:

$$D_i^{\pm} f(x) = f(c_i^{\pm}) - f(x) \quad \text{and} \quad D^{\pm} f(x) = \begin{pmatrix} D_1^{\pm} f(x) \\ \vdots \\ D_d^{\pm} f(x) \end{pmatrix}.$$

Finally, we use the customary notation ∇ for the gradient of a function, and we denote the scalar product of two vectors u, v as $\langle u, v\rangle$. Moreover, given a vector function F with components F_i, $i = 1, \ldots, d$, we write $\langle \nabla, F(x)\rangle = \sum_{i=1}^{d} \frac{\partial}{\partial x_i} F_i(x)$ the divergence of F.

THEOREM 2. *The family $(T_t)_{t\geq 0}$ is a Markov semigroup that satisfies the Feller property, that is, $T_t(C(E)) \subset C(E)$ for all $t \geq 0$ and $\lim_{t\to 0} \|T_t f - f\|_\infty = 0$, where $\|\cdot\|_\infty$ denotes the uniform norm of the Banach space $C(E)$ of all continuous functions defined on E. Moreover, this semigroup has an infinitesimal generator L with a domain $D(L)$ which includes all C^2-functions $f : E \to \mathbb{R}$, and*

$$\begin{aligned} Lf(x) \;=\; & \frac{1}{2}\sum_{i=1}^{d} \gamma_i x_i (1 - x_i) \frac{\partial^2}{\partial x_i^2} f(x) \\ & + \sum_{i=1}^{d} \left(\sum_{j=1}^{d} (a_{j,i}(x) - a_{i,j}(x)) x_j - a_{i,i}(x) x_i \right) x_i \frac{\partial}{\partial x^i} f(x) \\ & + \sum_{i=1}^{d} p_i \left(f(c_i^+(x)) - f(x) \right) + \sum_{i=1}^{d} q_i \left(f(c_i^-(x)) - f(x) \right). \end{aligned} \tag{18}$$

As a result, $f(t, x) := T_t f(x)$ satisfies the backward Kolmogorov equation:

$$\frac{\partial}{\partial t} f(t, x) = Lf(t, x). \tag{19}$$

In short-hand notation, for any $f \in C^2(\overset{o}{E})$, the generator is written as

$$\begin{aligned} Lf(x) \;=\; & \frac{1}{2}\langle \sigma(x)\sigma(x)^T \nabla, \nabla f(x)\rangle + \langle x \bullet (A_0^T(x) - A(x))x, \nabla f(x)\rangle \\ & + \langle p, D^+ f(x)\rangle + \langle q, D^- f(x)\rangle. \end{aligned}$$

Proof. This theorem is indeed a consequence of the fact that all Lévy processes define Feller semigroups; however, we provide here a direct proof. Let $\mathbf{P}_x^N$ denote the probability distribution of the solution to (5) starting from $x \in E$, when $\sigma(x)$ is replaced by its Bernstein approximation $\sigma^{(N)}(x)$. Then, as proved in [19, Thms. 6.4.5 and 6.4.6], the family $T_t^N f(x) = \mathbf{E}_x^N(f(X(t)))$ is a homogeneous Markov semigroup. This is indeed a consequence of a measurability property of the map $x \mapsto \mathbf{P}_x^N$ in the following sense. Recall that Ω is the Polish space of *cadlag* functions with the Skorokhod topology. The set $\Pi(\Omega)$ of probabilities on Ω is endowed with the weak topology of measures, and $\mathcal{B}(\Pi(\Omega))$ is the associated Borel σ-field. So, $x \mapsto \mathbf{P}_x^N$ is $\mathcal{B}(\Pi(\Omega))$-measurable.

Since $\mathbf{P}_x^N$ converges to $\mathbf{P}_x$ in the weak topology of probability measures on the Polish space Ω, then given any bounded continuous function F, $\mathbf{P}_x^N(F) = \int_\Omega F d\mathbf{P}_x^N \to$

$\mathbf{P}_x(F) = \int_\Omega F d\mathbf{P}_x$ as $N \to \infty$. As a result, the map $x \mapsto \mathbf{P}_x$ is $\mathcal{B}(\Pi(\Omega))$-measurable as well. Therefore, $(T_t)_{t\geq 0}$ is a homogeneous Markov semigroup, too.

The form of the generator (18) follows from a straightforward and customary application of Itô's formula to the process X under the probability $\mathbf{P}_x$.

Let L^N denote the generator of the semigroup $(T_t^N)_{t\geq 0}$ which is indeed of the same form (18) but with $\sigma_i^2(x)$ replaced by $\sigma_i^{(N)2}(x)$. $(T_t^N)_{t\geq 0}$ is a Feller semigroup as a consequence of Theorem 6.7.2 in [19], because the coefficients of the corresponding stochastic differential equation are continuous and uniformly bounded on the compact set E.

Notice that $T_t(C(E)) \subset C(E)$ if and only if for all $f \in D(L)$, it holds that $Lf \in C(E)$. Then, by a density argument, it suffices to prove that $Lf \in C(E)$ for all $f \in C^2(\overset{o}{E})$. Now, due to the compactness of E and the uniform convergence of the Bernstein approximation of $\sigma(x)$, it holds that

$$\sup_{x\in E} \left|L^N f(x) - Lf(x)\right| \leq \left\|\sigma^{(N)2}(x) - \sigma^2(x)\right\|_\infty \|\Delta f\|_\infty < \infty. \tag{20}$$

As a result $Lf \in C(E)$, since $L^N f$ does. Moreover, using that all T_t are contractions, the definition of the generator, the fact that $Lf \in C(E)$, and the compactness of E,

$$\|T_t f - f\|_\infty \leq \int_0^t \|Lf\|_\infty \, ds \leq t \|Lf\|_\infty ; \tag{21}$$

therefore, $\lim_{t\to 0} \|T_t f - f\|_\infty = 0$. As a result, the semigroup is Feller. ∎

Compactness of E allows us to obtain additional properties for our model. There exist in particular regular conditional probabilities, so that the semigroup can be represented as

$$T_t f(x) = \int_E P_t(x, dy) f(y) \tag{22}$$

for all bounded Borel functions on E, where $P_t(x, dy) = \mathbf{P}_x(X_t \in dy)$ is a Markov transition probability kernel.

The dual space of the Banach space $C(E)$ is the space of Radon measures $M(E) = C(E)^*$. Thus, one defines the dual semigroup $(T_t^*)_{t\geq 0}$ acting on a measure $\mu \in M(E)$ by the equality

$$\int_E T_t^* \mu(dx) f(x) = \int_E \mu(dx) T_t f(x) = \int_E \mu(dx) \int_E P_t(x, dy) f(y) \quad (f \in E). \tag{23}$$

Further, a measure μ is invariant if $T_t^* \mu = \mu$ for all $t \geq 0$, that is, $\int_E \mu(dx) T_t f(x) = \int_E \mu(dx) f(x)$.

For any $x \in E$, $(P_t(x, \bullet))_{t\geq 0}$ is a family of probability measures on the compact set E, so they are relatively weakly compact or tight. And, any limit point is an invariant measure. Therefore, in our case we have the following.

COROLLARY 2. *There exists at least an invariant probability measure under the action of the dual semigroup* $(T_t^*)_{t\geq 0}$.

3.3. Stability: Conditions for recurrence in 0 (extinction of species). Within this section we look for sufficient conditions to have the extinction of a subpopulation $(X_i(t, \omega); i \in I)$ of species $(I \subset \{1, \ldots, d\})$. Consider the following additional

hypothesis on the rate functions of our model:

$$\text{(Ext(I))} \qquad \begin{cases} \text{For any } x \in E \text{ and all } i \in I, \text{ the following inequality holds:} \\ \displaystyle\sum_{j=1}^{d} (a^0_{j,i}(x) - a_{i,j}(x))x_j + (p_i - q_i)m_i \leq 0. \end{cases}$$

To analyze the recurrence in 0 of the biomass flow $X_i(t,\omega)$ for all $i \in I$, we consider the stopping times

$$D^I_r(\omega) := \inf\left\{ t \geq 0 : \left[\sum_{i \in I} |X_i(t,\omega)|^2 \right]^{1/2} \leq r \right\} \quad (0 < r < 1) \tag{24}$$

and

$$\tau_I(\omega) = \inf\{t \geq 0 : \ X(t,\omega) = 0, \ i \in I\}. \tag{25}$$

THEOREM 3. *Under the hypothesis* (Ext(I)), *it holds that*

$$\mathbb{P}_x(D^I_r < \infty) = 1 \tag{26}$$

for all $x \in E$, all $0 < r < 1$. As a result, $\mathbb{P}_x(\tau_I < \infty) = 1$; that is, the species labeled by $i \in I$ go to extinction. If $I = \{1, \ldots, d\}$, then 0 is an absorption point for the whole Markov process $(X(t))_{t \geq 0}$, and all the population eventually disappears.

Proof. Assume there exists a vector $\lambda \in E$ such that $\lambda_i > 0$, $i \in \{1, \ldots, d\} \setminus I$, $\lambda_i = 0$ for $i \in I$, and $\sum_{i=1}^d \lambda_i = 1$. Define $V(x) = \langle \lambda, x \rangle$ $(x \in E)$. Let us define the stopping time $S_R(\omega) := \inf\{t \geq 0 : \ \langle \lambda, X(t,\omega) \rangle \geq R\}$. Since $X(t) \in E$ with probability 1, $S_R \to \infty$, $\mathbb{P}_x$-a.s. if $R \to \infty$ for all $x \in E$.

A straightforward computation shows that

$$\begin{aligned} LV(x) &= \langle \lambda, b(x) \rangle + \langle \lambda, (p-q) \bullet \eta(x) \rangle \\ &= \langle \lambda, b(x) + (p-q) \bullet \eta(x) \rangle \\ &= \sum_{i=1}^{d} \lambda_i \left\{ x_i \left[\sum_{j=1}^{d} (a^0_{j,i}(x) - a_{i,j}(x))x_j + (p_i - q_i)m_i \right] \right\} \\ &\leq 0. \end{aligned}$$

From Itô's formula we obtain that the process $V(X(t))$ is a positive supermartingale. By Doob's stopping theorem, we obtain

$$V(x) \geq \mathbb{E}_x(V(X(S_R \wedge D_r))) \geq \int_{\{S_R < D_r\}} V(X(S_R)) d\mathbb{P}_x = R\,\mathbb{P}_x(S_R < D_r).$$

Therefore, $\mathbb{P}_x(S_R < D_r) \leq V(x)/R$. Now, letting $R \to \infty$, we obtain $\mathbb{P}_x(D^I_r = \infty) = 0$, so that $\mathbb{P}_x(D^I_r < \infty) = 1$.

Clearly, $D^I_r \leq \tau_I$ for all $0 < r < 1$, so that the supermartingale property and Doob's theorem imply again that

$$\begin{aligned} V(x) &\geq \mathbb{E}_x(V(X(S_R \wedge D^I_r))) \\ &\geq \mathbb{E}_x(V(X(S_R \wedge \tau_I))) \\ &\geq \int_{\{S_R < \tau_I\}} V(X(S_R)) d\mathbb{P}_x \\ &= R\,\mathbb{P}_x(S_R < \tau_I). \end{aligned}$$

Thus, letting $R \to \infty$ yields $\mathbb{P}_x(\tau_I = \infty) = 0$, so that τ_I is finite almost surely, which means that all species labeled by $i \in I$ go extinct.

If $I = \{1, \ldots, d\}$, this implies that $X(t)1_{\{t>\tau_I\}} = 0$ almost surely. That is, 0 is absorbing for the biomass flow, so there is extinction of all the species in a finite time $\tau_{\{1,\ldots,d\}}$. ∎

4. Examples and simulations. For the numerical examples, we consider networks classified into three level sets: basal species, which commonly correspond to autotrophs or primary producers, intermediate species, which can be considered herbivores, and a top carnivorous species. We consider that the trophic biomass transfer from species i to j ($i \to j$) is given by the following coefficient function (cf. section 2.2):

$$g_{ij}(u) = \frac{A_{ij}}{1 + B_{ij}u},$$

where $A_{ij} > 0$ denotes the attack rate (including searching, pursuing, and capturing) and $B_{ij} > 0$ denotes the handling time (including consumption) of the j-species with respect to the i-species, respectively. In addition, we consider constant "death" (biomass loss) rates D_i, which can be viewed as a basal metabolic rate necessary for the organism maintenance. We assume that basal organisms generate their own biomass, and therefore this biomass generation, in the absence of consumption, is taken as a negative death rate $D_i < 0$, while for heterotrophs it is taken as a positive death rate $D_i > 0$, indicating that they do not generate their own energy. In our context, trophic interactions are represented through the following matrix function $A(x)$ (see section 2.2):

$$a_{ij}(x) = \begin{cases} D_i/x_i & \text{if } i = j, \\ g_{ij}(x_i) & \text{if } i \to j. \end{cases}$$

We note that this general trophic interaction model can be easily extended to non-trophic interactions, as shown in section 4.1.

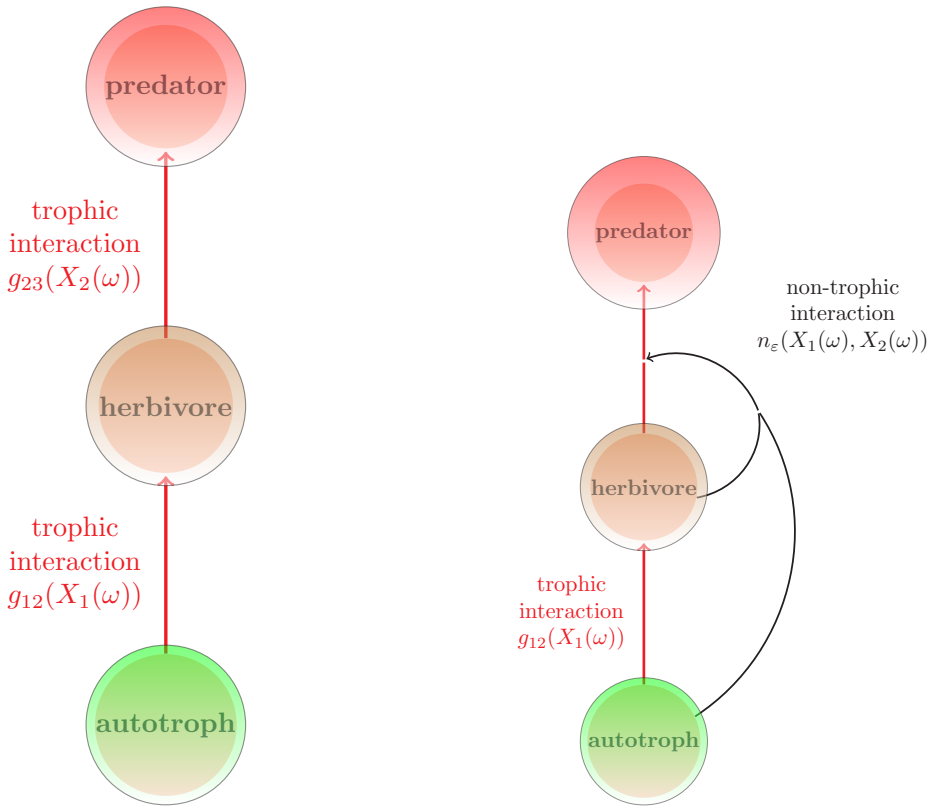
4.1. A three-species model. To illustrate the dynamic attributes and flexibility of this general framework, as a first example, we consider two types of three-species open-system models representing ecological networks with three interacting species: an autotroph (x_1), an herbivore (x_2), and a top predator (x_3) (see Figure 1). In the figure, model (a) represents a canonical tri-trophic food web (TI) used in many food web theoretical studies (e.g., [22]). Model (b) includes, in addition to the trophic interactions, a non-trophic one (NTI), where the autotroph modifies the interaction between the predator and herbivore, for instance, through providing refuge.

The non-trophic interaction in model (b) is represented by a coefficient function $n_\varepsilon(x_1, x_2) = \exp(-\varepsilon x_1) g_{23}(x_2)$ representing an exponential decay of the attack coefficient for the predator in the presence of the autotroph.

Remark 1. Notice that, for $\varepsilon = 0$, one recovers model (a), since $n_0(x_1, x_2)$ represents a trophic relation between the heterotrophs. In fact, $n_0(x_1, x_2) = g_{23}(x_2)$.

The corresponding matrix $A(x)$ representing the biomass transfer coefficients $a_{i,j}(x)$ is given in Table 1.

Remark 2. A straightforward computation shows that, under the above assumptions, the ith species satisfies the hypothesis (Ext(I)) if the condition number cond_i



(a) **TI model:** Trophic interactions only.

(b) **NTI model:** An NTI affects the attack rate of the top predator.

FIG. 1. *Three-species submodules of a metacommunity: $X_i(\omega, t)$, $i = 1, 2, 3$, are, respectively, the biomasses of the autotroph, the herbivore, and the top predator, engaged in strictly and exclusively consumptive or trophic interactions (TI model* (a)*) and in trophic as well as non-trophic interactions (NTI model* (b)*). The NTI can be visualized as refuges from predation provided by the autotroph.*

TABLE 1
$A(x)$ matrix for the three-species network submodule.

Matrix $A(x)$		
D_1/x_1	$g_{12}(x_1)$	0
0	D_2/x_2	$n_\varepsilon(x_1, x_2)$
0	0	D_3/x_3

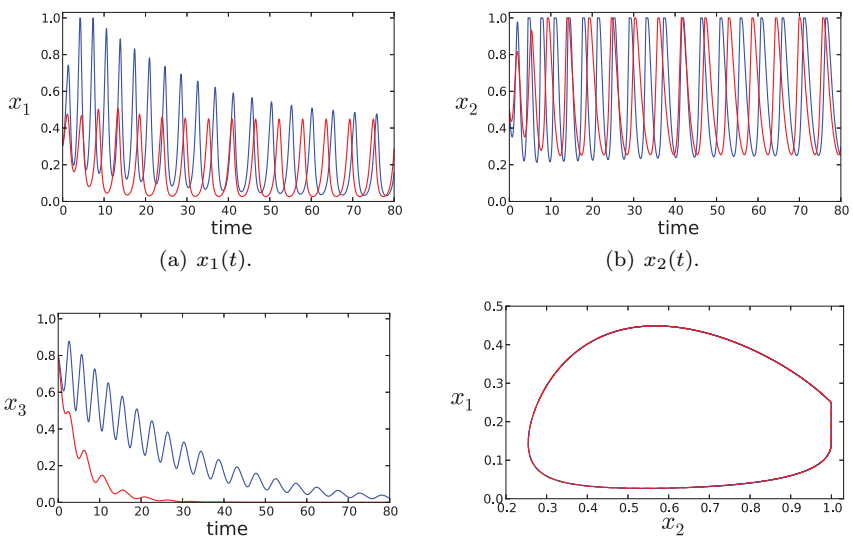
is nonpositive, where

$$\text{cond}_1 = -D_1 - (1 - 2p_1)m_1, \quad \text{cond}_i = A_{(i-1)i} - D_i + (1 - 2p_i)m_i \quad \text{for } i = 2, 3.$$

For the numerical simulations, we consider the parameter values given in Table 2. For the NTI models, we additionally consider (in all cases) $\varepsilon = 0.8$. When incorporating the environmental effects, we consider (in all cases) the diffusion coefficients $\gamma = [0.0001, 0.001, 0.01]$ and 10000 independent samples to estimate the MRA. Furthermore, to avoid trivial extinctions (see Remark 2), we consider several cases of migration rates m_i, with probabilities p_i, which are detailed below. Finally, results

TABLE 2
Predator attack coefficients (A_{ij}), prey handling times (B_{ij}), death rates (D_i), and initial conditions ($X_i(0)$) used in the simulations.

A_{ij}	B_{ij}	D_i	$X_i(0)$
		$D_1 = -0.19$	$X_1(0) = 0.3$
$A_{12} = 0.35$	$B_{12} = 0.1$	$D_2 = 0.05$	$X_2(0) = 0.5$
$A_{23} = 0.2$	$B_{23} = 0.7$	$D_3 = 0.08$	$X_3(0) = 0.8$



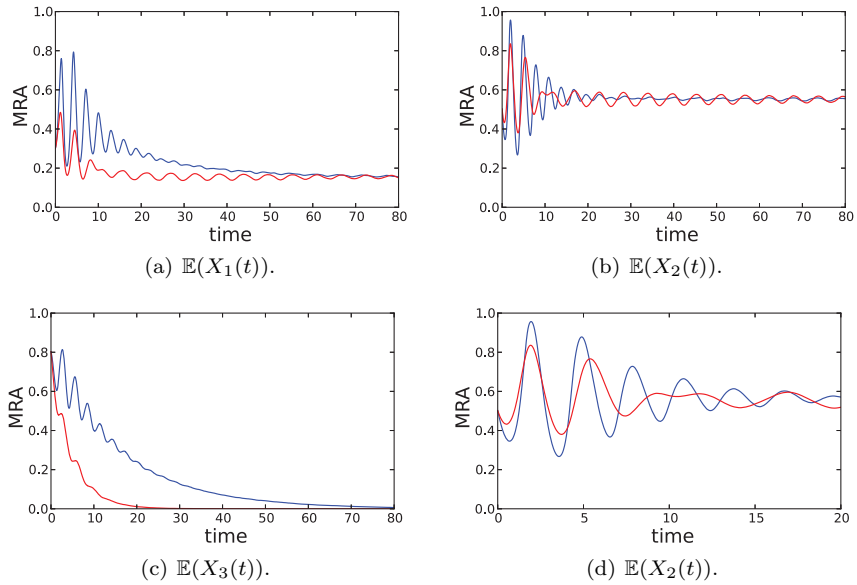
(a) $x_1(t)$. (b) $x_2(t)$. (c) $x_3(t)$. (d) $x_2(t)$ vs. $x_1(t)$.

FIG. 2. (a)–(c) *Bounded temporal dynamics of the biomass flow of each species in the absence of noise for the TI (blue) and NTI (red) models.* (d) x_2 *vs.* x_1 *plot of the closed unstable cycle obtained starting from a sufficiently large generational time in both models.*

are expressed in terms of the predator generations, i.e., time scaled by D_3.

First we notice that under the assumption of a closed network set of interactions, i.e., in the absence of noise, the particular election of parameters given in Table 2 generates rapid, large periodic oscillations of the autotroph and herbivore, and the extinction of the carnivore (Figures 2(a)–(c)). That is, the closed system is dramatically unstable. Apart from the fact that the carnivore goes extinct faster when an NTI is included in the model (Figure 2(c)), the existence of the non-trophic interaction does not alter model behavior or final conclusions. It should also be noted not only that the closed system shows periodic oscillations (Figure 2(d)), but that the trajectory of x_2 is not smooth, i.e., the dynamics is not derivable.

The violent oscillation trajectories observed in these simple model systems disappear when considering the interaction with the environment, i.e., when opening the system by adding noise (Figures 3–5). As can be appreciated in Figure 3, simply considering a small perturbation of $m_i = 0.001$ with probabilities $p_i = 0.5$, for $i = 1, 2, 3$, qualitatively changes the model behavior, generating dampened smooth oscillations (cf. Figure 3(d)) of the mean proportion of biomass flow, or mean relative abundance (MRA), i.e., both autotroph and herbivore coexist stably (Figures 3(a),(b)). Very small levels of migration, with equal probability of emigration or immigration, help stabilize trajectories but are not sufficient to rescue the carnivore from extinction.



(a) $\mathbb{E}(X_1(t))$. (b) $\mathbb{E}(X_2(t))$.

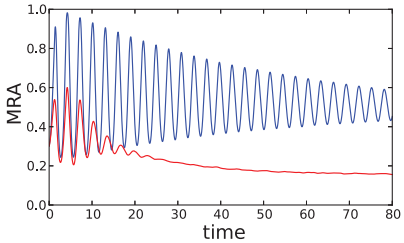
(c) $\mathbb{E}(X_3(t))$. (d) $\mathbb{E}(X_2(t))$.

FIG. 3. (a)–(c) *Mean temporal dynamics of the biomass flow of each species, when noise is considered to reflect interactions with the environment, for the TI (blue) and NTI (red) models. Plots obtained considering migration rates* $m = (0.001, 0.001, 0.001)$ *with probability* $p = (0.5, 0.5, 0.5)$ *and* 10000 *independent samples.* (d) *Zoom of the mean temporal dynamic of the second species in the generational time interval* $[0, 20]$. *The time axis considers up to* 80 *generations of the predator species.* cond = [0.19, 0.3, 0.12].

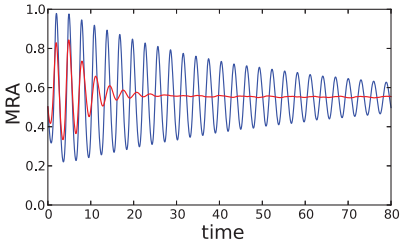
As in the closed-system case, the models with and without an NTI exhibit similar behaviors, although there is faster extinction of the carnivore when the autotroph reduces the carnivore's capture rate of the herbivore.

The importance of migration on local community dynamics is clearly depicted in Figures 4 and 5. In Figure 4, the same model systems are now examined under the rates of migration $m = (0.001, 0.001, 0.02)$ with probability $p = (0.5, 0.5, 0.98)$, i.e., with a high probability of immigration for the third species. This condition, where the population in a local community has a probability of infrequent but still positive immigration of biomass from the metacommunity, generates strikingly different behaviors. The local submodule of species exhibits damping oscillations towards a stable three-species configuration. Interestingly, these low levels of immigration are sufficient to allow coexistence of the top predator in the tri-trophic food web model, but not when an NTI is present (Figure 4(c)), highlighting the potential effects of NTIs in favoring or preventing local species coexistence. In Figure 5, we consider rates of migration $m = (0.15, 0.001, 0.001)$ with probability $p = (0.02, 0.5, 0.5)$, i.e., with a high probability of emigration for the autotroph species. Contrary to the previous example, here very similar dynamics are obtained for models with and without NTI, predicting a finite time of extinction for the herbivore and top predator, while a logistic-type asymptotic behavior is predicted for the autotroph. Further exploration of parameter space and of different types of interactions is needed to reach conclusions regarding the role of NTI in ecological networks.

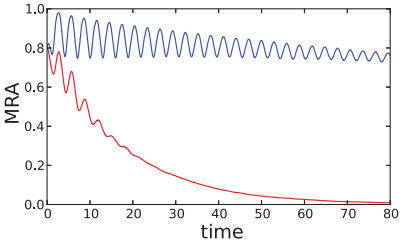
Notice that the numerical examples confirm that the (Ext(I)) hypothesis is only a sufficient condition for the extinction of the species. Indeed, Figure 5 shows that, even if not satisfied for any species, extinction for the herbivore and the predator



(a) $\mathbb{E}(X_1(t))$.

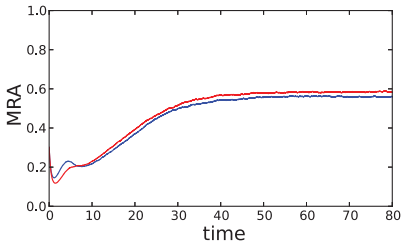


(b) $\mathbb{E}(X_2(t))$.

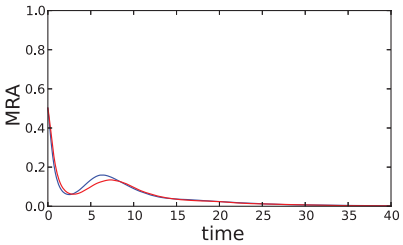


(c) $\mathbb{E}(X_3(t))$.

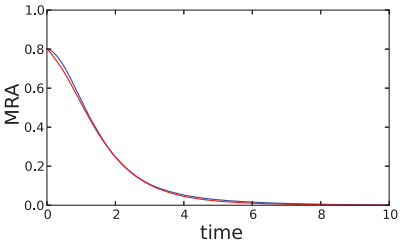
FIG. 4. (a)–(c) *Mean temporal dynamics of the biomass flow of each species for the TI (blue) and NTI (red) models. Plots obtained considering migration rates* $m = (0.001, 0.001, 0.02)$ *with probability* $p = (0.5, 0.5, 0.98)$ *and* 10000 *independent samples. The time axis considers up to* 80 *generations of the predator species.* cond = [0.19, 0.3, 0.1008].



(a) $\mathbb{E}(X_1(t))$.



(b) $\mathbb{E}(X_2(t))$.

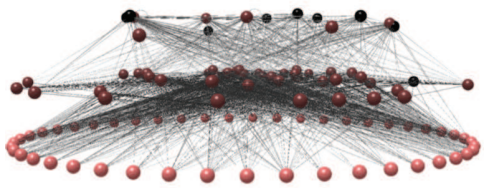


(c) $\mathbb{E}(X_3(t))$.

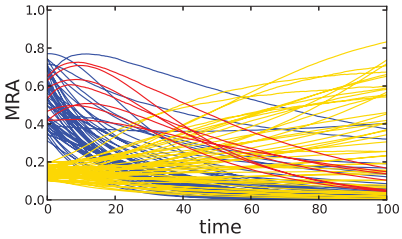
FIG. 5. *Mean temporal dynamics of the biomass flow of each species in the system for the TI (blue) and NTI (red) models. Plots obtained considering migration rates* $m = (0.15, 0.001, 0.001)$ *with probability* $p = (0.02, 0.5, 0.5)$ *and* 10000 *independent samples. In this case, autotroph biomass is exported from the system, leading to extinction of the herbivore and carnivore. The time axis considers up to* 80 *generations of the predator species.* cond = [0.046, 0.3, 0.12].

is possible, while Figures 3 and 4 show that extinction for the third species is also possible even if it is not satisfied for this species.

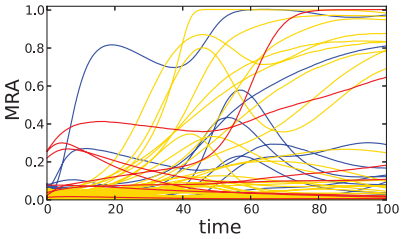
4.2. A complex network model. The ability of the proposed framework to model complex networks is demonstrated here by modeling a food web formed by 104 species of marine intertidal organisms (Figure 6(a)). The food web corresponds to the rocky intertidal community observed in wave-exposed rocky shore environments of central Chile, where most trophic interactions have been documented with an unusual level of detail (see [12]). For simplicity, we do not consider cannibalistic links. While modeling such large networks using deterministic approaches usually represents an important challenge (cf. [23, 25, 24, 26]), we show that the open-system approach can easily model this food web and allows for exploration of different parameter configurations leading in both simulations A and B in Figure 6 to coexistence of the great majority of species, albeit with contrasting trajectories.



(a) Intertidal food web.



(b) Simulation A.



(c) Simulation B.

FIG. 6. (a) *Representation of the intertidal food web composed of* 104 *species with a total of* 1346 *trophic interactions (see* [12] *for details).* (b) *Mean temporal dynamics for a simulation considering the set of parameters* A *in Table* 3. (c) *Mean temporal dynamics for a simulation considering the set of parameters* B *in Table* 3. *Yellow lines correspond to basal, blue to intermediate, and red to top species, respectively.*

5. Discussion. Our approach envisions ecological systems as open systems that are continuously being affected by nonobserved interactions with other species and the environment (see also [27, 28]), and which naturally lend themselves to the introduction of stochastic processes at the outset to model the basic evolution equations. It also includes in its foundations the notion that local systems are not isolated from regional processes such as migration, speciation, and nutrients flows [29, 18, 30].

The implications of the open-system approach are severalfold. First, it provides a different philosophical view of ecological community dynamics. While a fundamental characteristic of closed systems is their conservation of energy, open systems instead are inherently dissipative and irreversible. While closed systems presuppose that one knows every single variable affecting the system dynamics, the open-system paradigm takes it as a given that we will never be able to have a complete knowledge of the

TABLE 3

Parameter values used in the simulation of the complex network (Figure 6). Each species was randomly assigned a parameter value within the range specified in the table, and according to its trophic level. In model A, N_j *represents the total number of species consumed by the* j*-species. In both simulations, we consider the diffusion coefficients* γ_i *equal to* 0.0001, 0.001, *and* 0.01 *for basal, intermediate, and top species, respectively, and arbitrarily chosen migration rates* $m_i \in [0, 0.2]$, *with random probabilities* $p_i \in [0.4, 0.6]$.

Model A

	A_{ij}	B_{ij}	D_i	$X_i(0)$
Basal			$[-0.02, -0.002]$	$[0.1, 0.2]$
Intermediate	$[0, N_j^{-1}]$	$[0, 1]$	$[0.01, 0.06]$	$[0.3, 0.8]$
Top	$[0, N_j^{-1}]$	$[0, 1]$	$[0.01, 0.06]$	$[0.4, 0.7]$

Model B

	A_{ij}	B_{ij}	D_i	$X_i(0)$
Basal			$[-0.1, -0.002]$	$[0.001, 0.06]$
Intermediate	$[3, 4]$	$[0.2, 1.5]$	$[0.01, 0.06]$	$[0.002, 0.09]$
Top	$[6, 7]$	$[5, 10]$	$[0.01, 0.06]$	$[0.005, 0.3]$

phenomenon under study. Thus, it is crucial to distinguish between observable and nonobservable quantities. For instance, in our model, functions of the biomass of species in the focal system are observables (e.g., transfer functions α_{ij}), while the events of migrations, rapid fluctuations due to environmental changes, and speciation, among others, are not observables. This requires the use of *noises* to describe the interactions between the observed focal system and the unknown local and regional environment.

Second, from a mathematical point of view, there are many tools and extensive literature to deal with appropriate differential equations to describe closed systems, and to explore related concepts such as stability of solutions. The open-system approach proceeds via a dilation of basic spaces, i.e., adding a probability space to the set where the system dynamics takes place, introducing stochastic processes and their probability distributions. Thus, *stability* takes on a completely different meaning (see [44]). For open systems, the qualitative analysis focuses on the existence of invariant or stationary probability measures μ, and as we mention in our Corollary 2, in our case there exists at least one. However, to find an explicit expression for μ is a nontrivial task, which will be developed in a future contribution for some special classes of models. Moreover, not all stationary probabilities represent equilibrium distributions, which require additionally that there be zero entropy production or, equivalently, that the system become reversible [31, 32, 33].

Third, there are many ways to open a closed-system representation of nature, and this generally is much more involved than simply adding a noise term to standard differential equations. Indeed, one needs to look first for a characterization of the transfer of energy, mass, or information between the main system and the environment based on so-called first principles. For instance, the diffusion coefficient of the "logistic" form is inspired and developed from a neutral approach to a wide class of conveniently rescaled birth and death processes, which all converge to a similar diffusion (see [34], as well as [35, 36]). Yet, there is still room for improvement in this matter. Indeed, the use of the same diffusion coefficient in our model assumes that each species is suffering very frequent energy-mass interactions within the environment as a whole (including climate changes, temperature, and other species globally),

which depend only on their specific biomass. The effects of introducing short-time fluctuations through Wiener noises for each species separately must still be explored in more detail. Poisson noises model longer time scale interactions and have been used here to include migrations. Evidently, new refinements could consider more realistic approaches to these slow-pace processes in comparison to white noise, including, for instance, speciation through branching processes. The importance of different time scales in ecological dynamics is fundamental [37], and the stochastic framework proposed here provides a simple way of including time scale diversity into ecological networks of organisms interacting simultaneously in different ways among themselves and with their environment.

As we mentioned before, open systems are typically dissipative. This implies that in general species go extinct within the focal system, unless one includes explicitly a *recovery* force, such as the dynamics of the autotroph in our examples, which generates its own biomass through photosynthesis, or imports the biomass from the metacommunity or reservoir through immigration. Thus, in a number of cases this opening approach regularizes irregular or even chaotic trajectories when some models of species interactions are written as a closed system, like the tri-trophic food web model analyzed here. As we show, the same food web model, with or without NTI, produces smooth trajectories in the stochastic form. Moreover, if small levels of immigration are allowed, the model can produce stable coexistence of all species.

Random fluctuations are ubiquitous across living systems because of the probabilistic nature of the interactions underlying the transfer of energy, matter, and information, and because of the open nature of living systems, which in their inordinate complexity constrain us to work only with parts (e.g., main systems) instead of wholes. As already mentioned, everything else that affects the dynamics of the main system, and is not explicitly included in it, is envisioned as random environmental fluctuations or noises. During recent decades network theory has become a powerful approach to understanding the dynamics of matter, energy, and information across a wide diversity of complex systems [38], and stochastic approaches have become prominent in the analysis of gene and neural networks [39, 40] but less so in ecological systems. Part of the challenge of applying stochastic approaches to ecological networks lies in the variety of interactions and types of entities (the multilayer structure [41]) as well as in the several time scales involved. Our general stochastic framework is intended to alleviate these limitations.

To summarize, we contend that our approach provides a unified stochastic framework to deal with trophic and non-trophic interactions in open ecological networks. Our simulations are only intended to illustrate the capacity of the framework to model such interactions and observe population biomass trajectories. Further research is indeed needed to reach general conclusions regarding not only non-trophic interactions in ecological webs, but also the role of regional processes in ecological network attributes. To this end, the mathematical model as well as the corresponding codes developed here provide a suitable "virtual laboratory" to start analyzing different forms of trophic and non-trophic interactions, within realistically complex ecological webs, such as the ones that are now being empirically described [42, 43], a task that should occupy network ecologists in the coming years.

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REFERENCES

[1] L. von Bertalanffy, *The theory of open systems in physics and biology*, Science, 111 (1950), pp. 23–29.

[2] A. J. Lotka, *Analytical note on certain rhythmic relations in organic systems*, Proc. Natl. Acad. Sci. U.S.A., 6 (1920), pp. 410–415.

[3] A. J. Lotka, *Elements of Physical Biology*, Williams and Wilkins, Baltimore, 1925.

[4] V. Volterra, *Variazioni e fluttuazioni del numero da individui in specie animali conviventia*, Mem. Acad. Lincei Roma, 2 (1926), pp. 31–113.

[5] V. Volterra, *Variations and fluctuations of the number of individuals in animal species living together*, in Animal Ecology, R. N. Chapman, ed., McGraw-Hill, New York, 1931, pp. 408–409.

[6] R. May, *Stability and Complexity in Model Ecosystems*, Princeton University Press, Princeton, NJ, 2001.

[7] R. May, *Stability in randomly fluctuating versus deterministic environments*, Amer. Nat., 107 (1973), pp. 621–650.

[8] R. M. Anderson, D. M. Gordon, M. J. Crawley, and M. P. Hassell, *Variability in the abundance of animal and plant species*, Nature, 296 (1982), pp. 245–248.

[9] R. May, *Will a large complex system be stable?*, Nature, 238 (1972), pp. 413–414.

[10] A. Goudard and M. Loreau, *Nontrophic interactions, biodiversity, and ecosystem functioning: An interaction web model*, Amer. Nat., 171 (2008), pp. 91–106.

[11] S. Kéfi, E. L. Berlow, E. A. Wieters, S. A. Navarrete, O. L. Petchey, S. A. Wood, A. Boit, et al., *More than a meal... integrating non-feeding interactions into food webs*, Ecol. Lett., 15 (2012), pp. 291–300.

[12] S. Kéfi, E. L. Berlow, E. A. Wieters, L. N. Joppa, S. A. Wood, U. Brose, and S. A. Navarrete, *Network structure beyond food webs: Mapping non-trophic and trophic interactions on Chilean rocky shores*, Ecology, 96 (2015), pp. 291–303.

[13] A. Mougi and M. Kondoh, *Diversity of interaction types and ecological community stability*, Science, 337 (2012), pp. 349–351.

[14] O. Ovaskainen and B. Meerson, *Stochastic models of population extinction*, Trends Ecol. Evol., 25 (2010), pp. 643–652.

[15] O. Boettiger, *From noise to knowledge: How randomness generates novel phenomena and reveals information*, Ecol. Lett., 21 (2018), pp. 1255–1267, https://doi.org/10.1111/ele.13085.

[16] H.-P. Breuer and F. Petruccione, *The Theory of Open Quantum Systems*, Oxford University Press, New York, 2002.

[17] R. M. Nisbet and W. C. S. Gurney, *Modelling Fluctuating Populations*, Wiley, Chichester, 1982.

[18] S. P. Hubbell, *The Unified Neutral Theory of Biodiversity and Biogeography*, Princeton University Press, Princeton, NJ, 2001.

[19] D. Applebaum, *Lévy Processes and Stochastic Calculus*, 2nd ed., Cambridge University Press, Cambridge, UK, 2009.

[20] R. Rebolledo, *La méthode des martingales appliquée à l'étude de la convergence en loi de processus*, Bull. Soc. Math. France Mém., no. 62 (1979).

[21] J. Jacod, *Calcul Stochastique et Problèmes de Martingales*, Lecture Notes in Math. 714, Springer-Verlag, Berlin, 1979.

[22] A. Hastings and T. Powell, *Chaos in a three-species food chain*, Ecology, 72 (1991), pp. 896–903.

[23] J. Bascompte, C. J. Melián, and E. Sala, *Interaction strength combinations and the overfishing of a marine food web*, Proc. Natl. Acad. Sci. USA, 102 (2005), pp. 5443–5447.

[24] C. J. Melián, J. Bascompte, P. Jordano, and V. Krivan, *Diversity in a complex ecological network with two interaction types*, Oikos, 118 (2009), pp. 122–130.

[25] P. D. Roopnarine, *Ecological modeling of paleocommunity food webs*, in Conservation Paleobiology: Using the Past to Manage for the Future, The Paleontological Society Papers 15, G. P. Dietl and K. W. Flessa, eds., The Paleontological Society, Boulder, CO, 2009, pp. 195–220.

[26] D. B. Stouffer and J. Bascompte, *Compartmentalization increases food-web persistence*, Proc. Natl. Acad. Sci. USA, 108 (2011), pp. 3648–3652.

[27] S. A. Levin, *The role of theoretical ecology in the description and understanding of populations in heterogeneous environments*, Amer. Zool., 21 (1981), pp. 865–875.
[28] P. L. Chesson and R. R. Warner, *Environmental variability promotes coexistence in lottery competitive systems*, Amer. Nat., 117 (1981), pp. 923–943.
[29] S. Wright, *Evolution in Mendelian populations*, Genetics, 16 (1931), pp. 97–159.
[30] R. E. Ricklefs, *Community diversity: Relative roles of local and regional processes*, Science, 235 (1987), pp. 167–171.
[31] L. Onsager, *Reciprocal relations in irreversible processes.* I., Phys. Rev., 37 (1931), pp. 405–426.
[32] F. Fagnola and R. Rebolledo, *From classical to quantum entropy production*, in Quantum Probability and Infinite Dimensional Analysis, QP–PQ: Quantum Probab. White Noise Anal. 25, World Scientific, Hackensack, NJ, 2010, pp. 245–261.
[33] F. Fagnola and R. Rebolledo, *Entropy production for quantum Markov semigroups*, Comm. Math. Phys., 335 (2015), pp. 547–570.
[34] P. A. Marquet, G. Espinoza, S. Abades, A. Ganz, and R. Rebolledo, *On the proportional abundance of species: Integrating population genetics and community ecology*, Sci. Rep., 7 (2017), 16815, https://doi.org/10.1038/s41598-017-17070-1.
[35] M. Turelli, *Stochastic Community Theory: A Partially Guided Tour*, in Mathematical Ecology (Miramare-Trieste, 1982), Springer, Berlin, Heidelberg, 1986, pp. 321–339.
[36] M. Turelli, *Random environments and stochastic calculus*, Theoret. Population Biology, 12 (1977), pp. 140–178.
[37] S. A. Levin, *The problem of pattern and scale in ecology: The Robert H. MacArthur Award Lecture*, Ecology, 73 (1992), pp. 1943–1967.
[38] R. Albert and A.-L. Barabási, *Statistical mechanics of complex networks*, Rev. Modern Phys., 74 (2002), pp. 47–97.
[39] J. Karbowski, *Optimal wiring principle and plateaus in the degree of separation for cortical neurons*, Phys. Rev. Lett., 86 (2001), pp. 3674–3677.
[40] J. Paulsson, *Summing up the noise in gene networks*, Nature, 427 (2004), pp. 415–418.
[41] M. Kivela, A. Arenas, M. Barthelemy, J. P. Gleeson, Y. Moreno, and M. A. Porter, *Multilayer networks*, J. Complex Networks, 2 (2014), pp. 203–271.
[42] R. Beas-Luna, M. Novak, M. H. Carr, M. T. Tinker, A. Black, J. E. Caselle, M. Hoban, D. Malone, and A. Iles, *An online database for informing ecological network models: http://kelpforest.ucsc.edu*, PLoS One 9 (2014), e109356, https://doi.org/10.1371/journal.pone.0109356.
[43] E. L. Sander, J. T. Wootton, and S. Allesina, *What can interaction webs tell us about species roles?*, PLoS Comput. Biol., 11 (2015), e1004330.
[44] H.-R. Gregorius, *The notion of stability in open dynamical systems from an ecological perspective*, Internat. J. Gen. Systems, 30 (2001), pp. 347–378.