



Improved stability indicators for empirical food webs



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ABSTRACT

After a short review of the contemporary stability indicators recently used to assess behavior of the empirical food webs, we discuss the corresponding amplification and timescales of transient instability. Then, a novel robust measure that incorporates uncertainty level of empirical data and amplification–timescale frame in the stability analysis is introduced. As a result, more realistic notion of stability is achieved, and its usefulness is advocated. Finally, an efficient numerical algorithm for its computation is constructed to allow possible applications to high resolution food webs in the future. New stability indicator is computed for the soil food web and it is compared with the ones reported in the literature.

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1. Introduction

One of the contemporary paradigms developed to understand interplay between stability and complexity of the soil ecosystem is a mechanistic model of an energetic food web which consists of living organic matter (plants, animals, bacteria, fungi, etc.) and non-living organic matter (detritus with allochthonous and autochthonous source), see Moore and de Ruiter (2012). Based on the predator–prey coupling between functional groups, this dynamical systems approach provided important insights in Neutel et al. (2002, 2007). However, as we show in this paper, the methods used to assess stability have certain drawbacks and can be misleading. The main issue occurring in the studies we review is that the computed measures of stability correspond only to the asymptotically stable behavior of the linearization of the dynamical system. In other words, assessed stability is quite unrealistic, since natural systems are subject to environmental change and stochastic disturbances, and their structure and dynamics may never settle to behavior predicted by model asymptotics. Instead, populations and communities may show transient amplification that is due to *nonnormal* community matrices, cf. Townley et al. (2007), responsible for strange system behavior that defies explanation using eigenvalues, cf. Trefethen and Embree (2005). Therefore, we propose another theoretical indicator for the (robust) stability, which allows one to incorporate the level of uncertainty (errors in measurements, stochastic fluctuations, etc.) in empirical data, as

well as the timescale for possible transitional instabilities and the maximal amplification of initial perturbations. In addition, a novel efficient numerical algorithm is constructed to compute such measure and allow researchers to analyze their empirical data of food webs. Although the use of this new method is illustrated on a small size soil food web (low resolution), due to the used computational approach, the same algorithm can be used for large-scale empirical food webs (high resolution), as well. While in this paper the new stability indicator is introduced, discussed and justified in detail, its application on a large variety of empirical food webs and consequent ecological implications remain for further studies.

2. Materials and methods

2.1. Governing equations of material-flux networks

Following the research in Moore and de Ruiter (2012) and references therein, we consider a food web of $n \in \mathbb{N}$ functional groups of living species with the pool of non-living organic matter whose energy (as a common currency of the biomass, usually measured as the level of carbon or nitrogen) flow is approximately driven by the generalized Lotka–Volterra equations.

To introduce the model, for $i \in \mathcal{N} := \{1, 2, \dots, n\}$ denote the density of biomass (for soil food webs, the unit is typically gram of carbon (or nitrogen) per hectare per centimeter of depth) at time $t \geq 0$ of the i th functional group by $x_i(t)$, while the density of biomass in the detritus form is denoted by $x_{n+1}(t)$.

Furthermore, denote the sets of indices corresponding to the similar functional groups as \mathcal{P} – primary producers (plants, etc.), \mathcal{C} – primary consumers (herbivores, fungivores, bacteriovores and

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carnivores) and \mathcal{D} – detritivores (detritus consumers like certain fungi, bacteria, etc.). Thus, obviously, $\mathcal{N} = \mathcal{P} \cup \mathcal{C} \cup \mathcal{D}$.

Next, for $i \in \mathcal{P}$, let $g_i > 0$ be the growth rate of a primary producer, while for $i \in \mathcal{N}$, $b_i > 0$ is defined as the death rate of the species due to reasons other than predation, $a_i \in (0, 1)$ is its energetic assimilation efficiency and $p_i \in (0, 1)$ is its production efficiency. While density independent intrinsic increment rates g_i and decrement rates b_i , understood as units per time, are characteristics of species based on its history and/or its physiology, the energetic efficiency of the trophic interaction $e_i = a_i p_i$ represents the ratio of immobilized matter or energy that forms new biomass in the form of growth and reproduction to the amount of the matter or energy consumed. In that setting, the assimilation efficiency is defined as the ratio of the assimilated consumption (an intake of molecules through the cellular membranes so they can be used for growth, reproduction and maintenance) to the total amount of consumed biomass, while the production efficiency is defined as the ratio of the assimilated biomass used for production (growth and reproduction) to the total amount of the assimilated biomass.

Finally, since the model we investigate includes the biomass of nonliving organic matter that enters the system from the exterior, we will define $g_D \geq 0$ as the growth rate of biomass from such an allochthonous source in units per time.

The exchange of energy between the species is modelled by functional responses. Namely, for each consumer $j \in \mathcal{C}$, the characteristic of how it adapts to the changes of density of biomass in its prey $i \in \mathcal{P}$ in time t is given by $f_j(x_i(t))$. The simplest form of functional response assumes that the attack rate is constant regardless of the prey density, which leads to the linear function $f_j(x_i(t)) = c_{ij} x_i(t)$, where $c_{ij} \geq 0$ represents the consumption coefficient with the unit per biomass per time. In case when there is no trophic interaction, this coefficient is set to zero, i.e., $c_{ij} = 0$. The similar holds for detritivores $j \in \mathcal{D}$ where $f_j(x_{n+1}(t)) = c_{n+1j} x_{n+1}(t)$ and $x_{n+1}(t)$ is the density of biomass in the detritus in time t .

Finally, for all functional groups of organisms, $i \in \mathcal{P} \cup \mathcal{C} \cup \mathcal{D}$, self limitation is taken into account as intraspecific competition, understood as a negative effect of the individual organisms to the growth and reproduction of the others in their functional group of species. This process is modelled as density dependent via the same type of functional response, in our case – linear, $f_i(x_i(t)) = c_{ii} x_i(t)$, where $c_{ii} > 0$ represents the degree of intraspecific competition and includes acquisition and utilisation of joint resources (prey, space, mates, light, essential nutrients, etc.).

Using these notations, the governing deterministic equations of the energy flow in the functional food web are the following:

$$\begin{aligned} \dot{x}_i &= g_i x_i - \sum_{j \in \mathcal{C}} f_j(x_i) x_j - f_i(x_i) x_i, \quad (i \in \mathcal{P}) \\ \dot{x}_i &= e_i \sum_{\substack{j \in \mathcal{N} \\ j \neq i}} f_i(x_j) x_j - b_i x_i - \sum_{\substack{j \in \mathcal{C} \\ j \neq i}} f_j(x_i) x_j - f_i(x_i) x_i, \quad (i \in \mathcal{C}) \\ \dot{x}_i &= e_i f_i(x_{n+1}) x_i - b_i x_i - \sum_{j \in \mathcal{C}} f_j(x_i) x_j - f_i(x_i) x_i, \quad (i \in \mathcal{D}) \\ \dot{x}_{n+1} &= g_D + \sum_{j \in \mathcal{N}} b_j x_j + \sum_{\substack{j \in \mathcal{C} \\ k \in \mathcal{N} \\ k \neq j}} (1 - a_j) f_j(x_k) x_j - \sum_{j \in \mathcal{D}} f_j(x_{n+1}) x_j. \end{aligned}$$

In case of linear functional responses, the dynamics follows the law:

$$\dot{x}(t) = \Phi(x(t)), \tag{1}$$

where $\Phi : \mathbb{R}^n \rightarrow \mathbb{R}^n$ is a nonlinear function defined by the matrix of trophic interactions $C = [c_{ij}] \in \mathbb{R}^{n+1, n+1}$ and parameters g_D, b_i, a_i , and $p_i (i \in \mathcal{N})$. Furthermore, C has the following block form, due to the partitioning of the functional groups of species into four index sets $\mathcal{C}, \mathcal{P}, \mathcal{D}$ and $\{n+1\}$, starting from the top predators downwards:

$$C = \begin{bmatrix} C[\mathcal{C}, \mathcal{C}] & 0 & 0 & 0 \\ C[\mathcal{P}, \mathcal{C}] & C[\mathcal{P}, \mathcal{P}] & 0 & 0 \\ C[\mathcal{D}, \mathcal{C}] & 0 & C[\mathcal{D}, \mathcal{D}] & 0 \\ 0 & 0 & C[\{n+1\}, \mathcal{D}] & 0 \end{bmatrix}, \tag{2}$$

where $C[\mathcal{U}, \mathcal{V}]$ is a matrix whose rows are indexed by set \mathcal{U} and columns by set \mathcal{V} . Furthermore, note that matrices $C[\mathcal{P}, \mathcal{P}]$ and $C[\mathcal{D}, \mathcal{D}]$ are diagonal, while the predator-prey interactions among the primary consumers are contained in the lower triangular matrix $C[\mathcal{C}, \mathcal{C}]$.

A typical example of such food webs is below-ground food web of Schiermonnikoog in the north of the Netherlands studied in Neutel et al. (2007), see Fig. 1.

Since dynamical system (1) is a nonlinear one, its stability is usually investigated at the equilibrium point as the local asymptotic stability, cf. Moore and de Ruiter (2012). Namely, the equilibrium point $x^* \in \mathbb{R}^{n+1}$ is defined as a state of the system in which the system stays once it achieves it. In other words, x^* is a state vector such that $\Phi(x^*) = 0$. An equilibrium state x^* is locally asymptotically stable if there exists $\delta > 0$ such that for every $x(0)$ that is in δ neighbourhood of the equilibrium x^* (i.e., $\|x^* - x(0)\| < \delta$), it holds that $\lim_{t \rightarrow \infty} \|x(t) - x^*\| = 0$. As it is widely known, this stability property is independent of the norm $\|\cdot\|$ used, and it is characterised by the spectrum of the Jacobian matrix of (1) in the state $x = x^*$. In the setting of the food webs, the Jacobian matrix is often referred to as the community matrix, cf. Moore and de Ruiter (2012).

However, knowing that perturbation of equilibrium $x(0)$ (i.e., $\|x(0) - x^*\| < \delta$ for some small $\delta > 0$) evolves at the time according to $\dot{x}(t) = Ax(t) + \mathcal{O}(\|x(t) - x^*\|^2)$, where \mathcal{O} denotes little-o asymptotic symbol, the starting perturbation propagates in time t with the factor approximated by $\|e^{tA}\|$, where the norm is the induced matrix norm by the original vector norm $\|\cdot\|$. Thus, realistic behavior of the system that has suffered a small perturbation at equilibrium state is represented by the amplification envelope $\phi_A(t) := \|e^{tA}\|$, $t \geq 0$. But, as Trefethen and Embree (2005) pointed out, for non-normal matrix A , the eigenvalues alone are not enough to explain the behavior of $\phi_A(t)$. Unlike the asymptotic stability, the behavior of $\phi_A(t)$ is, of course, norm-dependent. But, having in mind that we deal with biomass densities, we are much more interested in their evolution in a specific norm (usually Euclidean vector norm $\|x\|_2 := \sqrt{\sum_i |x_i|^2}$ or max-norm $\|x\|_\infty := \max_i |x_i|$), than in the abstract setting of asymptotics (corresponding to the existence of an abstract norm in which system will have “nice” behavior).

Therefore, to assess ecological stability, instead of using asymptotic stability only, we adapt it to another concept of stability that incorporates, both, short-time and long-time square deviation from the equilibrium. Namely, asymptotically stable dynamical system (1) will be considered as (M, T) -stable if its amplification envelope $\phi_A(t) := \|e^{tA}\|_2$ fits in the given amplification–timescale frame (M, T) , i.e.,

$$\begin{aligned} \max_{t \geq 0} \phi_A(t) &\leq M \quad (\text{amplification limit}), \\ \max_{t \geq T} \phi_A(t) &\leq e^{-1} \quad (\text{timescale limit}). \end{aligned}$$

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