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# A deeper insight into the equilibrium of biological and ecological networks

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**Abstract**
The equilibrium of biological and ecological networks is often studied using eigenvector-eigenvalue analyses in order to reckon steady/unsteady properties and trajectories. Although at equilibrium inputs equal outputs for all the system variables, network flows continue to happen. Therefore, in this study I face three underestimated topics of network equilibrium: equilibrium flows, equilibrium sensitivity and equilibrium what-if properties. Using an applicative example, I show here that these three topics add important details to the knowledge of network behaviour at equilibrium.

**Keywords** equilibrium flows; equilibrium sensitivity; equilibrium what-if; network equilibrium.

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## 1 Introduction

The stability analysis of dynamical networks is a well-established topic, both in ecology and in biology. The equilibrium of biological and ecological networks is often studied using eigenvector-eigenvalue analyses in order to compute their steady/unsteady properties and trajectories. Using a different perspective, Ferrarini (2015) demonstrated that early, or late, stability can be imposed to any kind of ecological and biological network. Ferrarini (2016a) showed that network stability can be imposed also locally, not only globally.

In this study, I face three underestimated topics of network equilibrium: equilibrium flows, equilibrium sensitivity and equilibrium what-if. Using an applicative example, I show that these three topics can add important details to the knowledge of network behaviour at equilibrium.

## 2 Mathematical Formulation

A generic ecological (or biological) system composed by a set **S** of $n$ interacting taxonomic resolutions (species, genera, family, etc.) or aggregated assemblages of taxa (e.g., phytoplankton) is

$$\frac{d\mathbf{S}}{dt} = \gamma(\mathbf{S}(t)) \tag{1}$$

where $S_i$ is the number of individuals (or the total biomass) of the generic *i-th* taxonomic resolution or assemblage of taxa.

If we also consider time-dependent inputs (e.g. species reintroductions) and outputs (e.g. hunting) from outside, we must write:

$$\frac{d\mathbf{S}}{dt} = \gamma(\mathbf{S}(t)) + \mathbf{I}(t) + \mathbf{O}(t) \tag{2}$$

with $\mathbf{I}(t) \geq 0$ and $\mathbf{O}(t) \leq 0$, and with initial values

$$\mathbf{S}_0 = <\mathrm{S}_1(0),\ \mathrm{S}_2(0)...\mathrm{S}_n(0)> \tag{3}$$

and co-domain limits

$$\begin{cases} \mathrm{S}_{1\min} \leq S_1(t) \leq \mathrm{S}_{1\max} \\ ... & \forall t \\ \mathrm{S}_{n\min} \leq S_n(t) \leq \mathrm{S}_{n\max} \end{cases} \tag{4}$$

Stability happens at time $t = T^{Eq}$ when

$$\begin{cases} \dfrac{dS_1}{dt} = 0 \\ ... \\ \dfrac{dS_n}{dt} = 0 \end{cases} \tag{5}$$

or, by relaxing Eq. 5, when

$$\begin{cases} \dfrac{dS_1}{dt} \leq \varphi \\ ... & \text{with } \varphi \to 0 \\ \dfrac{dS_n}{dt} \leq \varphi \end{cases} \tag{6}$$

### 2.1 Reckoning network flows at equilibrium

Although at equilibrium inputs equal outputs for all of the variables, network flows continue to happen in the form

$$\begin{cases} \dfrac{dS_1}{dt}^{EQ} = inputs_{S1}{}^{Eq} - outputs_{S1}{}^{Eq} = 0 \\ ... \\ \dfrac{dS_n}{dt}^{EQ} = inputs_{Sn}{}^{Eq} - outputs_{Sn}{}^{Eq} = 0 \end{cases} \tag{7}$$

thus one main question is the amount of inputs and outputs at equilibrium for each variable, and also their ratios if compared to the equilibrium values. In fact, if flows at equilibrium are high compared to equilibrium values, a small perturbation of the network can lead to great changes, and vice versa.

The flow amount at equilibrium for each generic variable $S_i$ is

$$Inputs_{Si}{}^{Eq} = \gamma(\mathbf{S}_{+}{}^{Eq}(t)) + \mathbf{I}^{Eq}(t) = outputs_{Si}{}^{Eq} = \left|\gamma(\mathbf{S}_{-}{}^{Eq}(t)) + \mathbf{O}^{Eq}(t)\right| \tag{8}$$

where $S_+^{Eq}$ is the set of variables with positive input to $S_i$, and vice versa for $S_-^{Eq}$.

For instance, in a simple linear dynamical system composed by species <A, B, C, D> with equilibrium values <a, b, c, d> and interactions upon A equal to <0.3, -0.4, -0.9, 0.6>, then

$$Inputs_{A}{}^{Eq} = 0.3*a + 0.6*d = outputs_{A}{}^{Eq} = \left|-0.4*b - 0.9*c\right| \tag{9}$$

Thus, for the generic variable $S_i$ the ratio between equilibrium flow and equilibrium value is

$$\frac{Inputs_{Si}{}^{Eq}}{{}^{Eq}_{Si}} = \frac{\gamma(\mathbf{S}_{+}{}^{Eq}(t)) + \mathbf{I}^{Eq}(t)}{{}^{Eq}_{Si}} = \frac{Outputs_{Si}{}^{Eq}}{{}^{Eq}_{Si}} = \frac{\left|\gamma(\mathbf{S}_{-}{}^{Eq}(t)) + \mathbf{O}^{Eq}(t)\right|}{{}^{Eq}_{Si}} \tag{10}$$

## 2.2 Reckoning network what-if at equilibrium

Another important issue is how and how much the network equilibrium values change if one network parameter (let's say $p$) changes. Network what-if analysis can disentangle the directionality and the degree of network change at equilibrium for a given change of each network parameter. It can be computed as follows

$$\frac{\Delta_{\%}\ \mathbf{S}^{Eq}}{\Delta_{\%}\ p} = \frac{\dfrac{\partial \mathbf{S}}{\mathbf{S}^{Eq}}}{\dfrac{dp}{p}} = \frac{\partial \mathbf{S}}{\mathbf{S}^{Eq}} * \frac{p}{dp} = \frac{\partial \mathbf{S}}{dp} * \frac{p}{\mathbf{S}^{Eq}} \tag{11}$$

In case we vary simultaneously two parameters $p$ and $q$, we must calculate

$$\frac{\Delta_{\%}\ \mathbf{S}^{Eq}}{\Delta_{\%}\ (p,q)} = \frac{\dfrac{\partial^2 \mathbf{S}}{\mathbf{S}^{Eq}}}{\dfrac{dp}{p}\ \dfrac{dq}{q}} = \frac{\partial^2 \mathbf{S}}{\mathbf{S}^{Eq}} * \frac{p}{dp} * \frac{q}{dq} = \frac{\partial^2 \mathbf{S}}{dp\ dq} \frac{p*q}{\mathbf{S}^{Eq}} \tag{12}$$

and so on for $m$ parameters.

## 2.3 Reckoning network sensitivity at equilibrium

If we densify what-if analysis at equilibrium by multiple simulated parameter changes, we have a sensitivity analysis. For example, we can vary 1000 times the parameter $p$ by a ±5%. In pseudo code:

$$\begin{cases} m = 0 \\ \text{Do} \\ \dfrac{\Delta_{\%}\mathbf{S}^{Eq}}{\Delta_{\%}\ p} \\ \text{with } dp \in [0.95*p,\ 1.05*p] \\ m = m+1 \\ \text{Until } m = 1000 \end{cases} \qquad (13)$$

**3 An applicative Example**

Let's consider the classic Lotka-Volterra predator-prey model (Lotka, 1925; Volterra, 1926). The Lotka-Volterra equations are a combination of first-order, non-linear, differential equations widely used to describe the dynamics of biological systems with two species interacting (one as a prey and the other as a predator).

The Lotka-Volterra model makes five assumptions about the environment and the dynamics of the two interacting species: 1) the prey population finds food at any times; 2) the food supply for the predator depends completely on the size of the prey population; 3) the rate of change of each population is proportional to its size; 4) during the interaction, the environment remains unvarying; 5) predators have unbounded appetency. Since differential equations are used, the solution is deterministic and continuous; this means that the generations of both the predator and prey continually overlap.

The nonlinear Lotka-Volterra model with logistic grow of the prey $S_1$ is a particular case of Eq.1, and it reads as follows

$$\begin{cases} \dfrac{dS_1}{dt} = \alpha S_1(1-\dfrac{S_1}{\kappa}) - \beta S_1 S_2 \\ \dfrac{dS_2}{dt} = \beta\gamma S_1 S_2 - \delta S_2 \end{cases} \qquad (14)$$

with initial values

$$\vec{S}_0 = <S_1(0),\ S_2(0)> \qquad (15)$$

and co-domain limits

$$\begin{cases} S_{1\min} \le S_1(t) \le S_{1\max} \\ S_{2\min} \le S_2(t) \le S_{2\max} \end{cases} \quad \forall t \qquad (16)$$

Let's consider the Lotka-Volterra system of Eq. 14 with the following parameters and constants:

$$\begin{cases} S_1(0) = 100 \\ S_2(0) = 20 \\ \alpha = 4 \\ \beta = 0.05 \\ \gamma = 1 \\ \delta = 4 \\ \kappa = 500 \\ dt = 0.01 \\ \varphi = 0.0001 \end{cases}$$

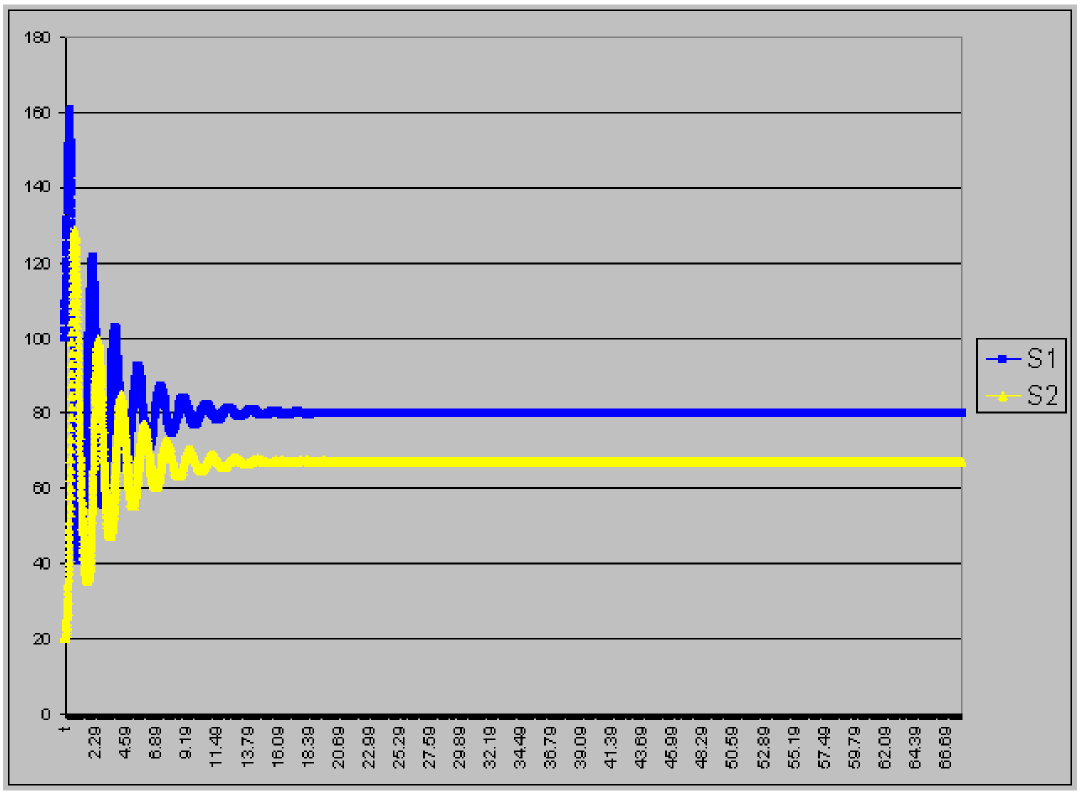

**Fig. 1** Time plot of the nonlinear Lotka-Volterra system under study.

This network has eigenvalues < –0.32 +3.65*i*, –0.32 -3.65*i* > which means that the equilibrium point is stable (both the real parts of the two eigenvalues are negative) with oscillations that reduce the amplitude while nearing the steady point (the sum of imaginary parts is 0). The previous system goes at the steady state with $S_1$ = 80.00 and $S_2$ = 67.20 (Fig. 1).

At equilibrium, the previous biological network has the following flows computed through Eq. 8:

$$Inputs_{S1}{}^{Eq} = 4*80*(1-80/500) = 268.8$$
$$Outputs_{S1}{}^{Eq} = -0.05*80*67.2 = -268.8$$
$$Inputs_{S2}{}^{Eq} = 0.05*80*67.2 = 268.8$$
$$Outputs_{S2}{}^{Eq} = 4*67.2 = -268.8$$

Thus, the ratios between flows and values at equilibrium are

$$\begin{cases} \dfrac{Inputs_{S1}{}^{Eq}}{{}_{S1}{}^{Eq}} = \dfrac{268.8}{80} = 3.36 \\ \dfrac{Inputs_{S2}{}^{Eq}}{{}_{S2}{}^{Eq}} = \dfrac{268.8}{67.2} = 4 \end{cases}$$

A two-parameter what-if analysis with α = 4.1 (instead of 4) and δ=3.8 (instead of 4), imposed exactly at network equilibrium $T^{Eq}$, produces the changes in network dynamics illustrated in Fig. 2 and Fig. 3 and computed using Eq. 11. It is very interesting to note the evident shift in the network equilibrium due to the post-equilibrium change in the α and δ parameters. All the analyses have been carried out using the software Control-Lab 8 (Ferrarini, 2016b).

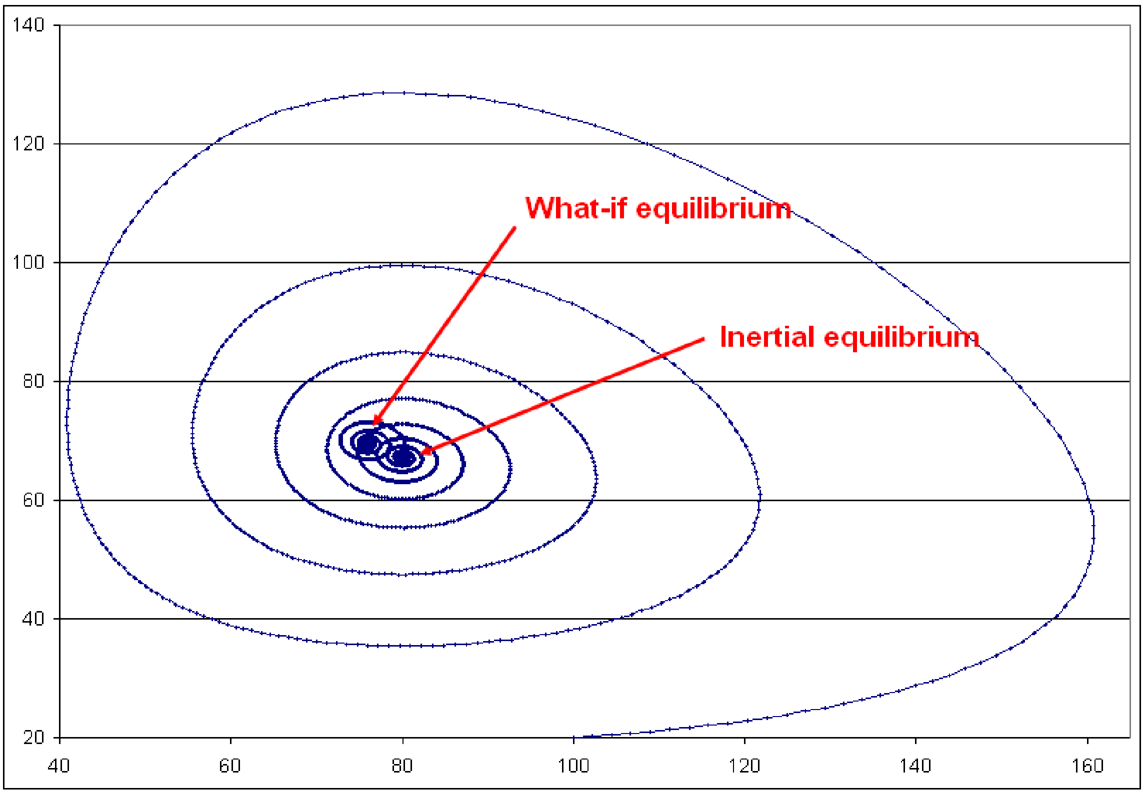


**Fig. 2** Two-parameter what-if analysis at equilibrium of the Lotka-Volterra system under study (phase plot).

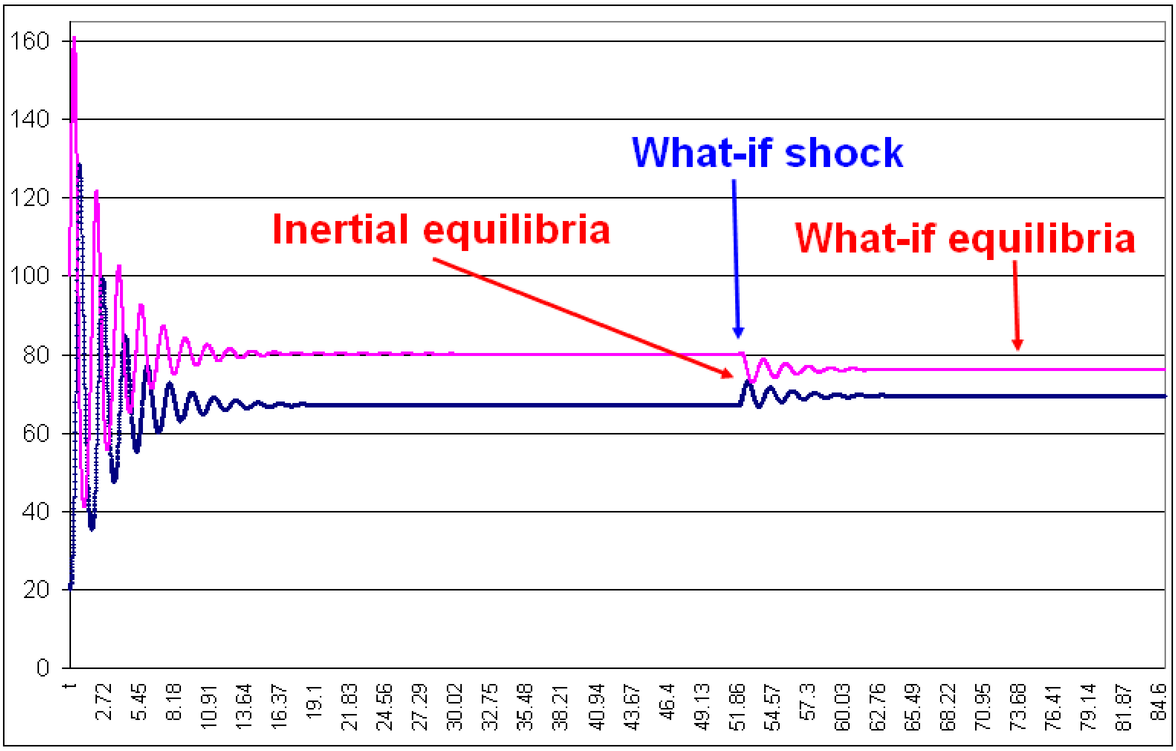


**Fig. 3** Two-parameter what-if analysis at equilibrium of the Lotka-Volterra system under study (time plot).

## 4 Conclusions

The equilibrium of dynamical networks is a well-studied topic both in ecology and in biology. In this paper, I have adopted a different perspective: instead of analyzing the stability of a generic biological or ecological network, I have focused on three underrated topics: equilibrium flows, equilibrium what-if analysis and equilibrium sensitivity analysis.

I have showed that these three topics provide useful details about the way a biological or ecological network behaves, thus providing a deeper perspective into the equilibrium of biological and ecological networks.

## References

Ferrarini A. 2015. Imposing early stability to ecological and biological networks through Evolutionary Network Control. Proceedings of the International Academy of Ecology and Environmental Sciences, 5(1): 49-56

Ferrarini A. 2016a. Bit by bit control of nonlinear ecological and biological networks using Evolutionary Network Control. Network Biology, 6(2): 47-54

Ferrarini A. 2016b. Control-Lab 8: a software for the application of Ecological Network Control. Manual, 106 pages

Lotka A.J. 1925. Elements of Physical Biology. Williams & Wilkins Co, Baltimore, USA

Volterra V. 1926. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. Mem. R. Accad. Naz. dei Lincei. Ser. VI, vol. 2