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A guideline to study the feasibility domain of multi-trophic and changing ecological communities

Chuliang Song[a], Rudolf P. Rohr[b], Serguei Saavedra[a,1,*]

[a] Department of Civil and Environmental Engineering, MIT, 77 Massachusetts Av., Cambridge, MA 02139, USA
[b] Department of Biology - Ecology and Evolution, University of Fribourg Chemin du Musée 10, Fribourg CH-1700, Switzerland

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ABSTRACT

The feasibility domain of an ecological community can be described by the set of environmental abiotic and biotic conditions under which all co-occurring and interacting species in a given site and time can have positive abundances. Mathematically, the feasibility domain corresponds to the parameter space compatible with positive (feasible) solutions at equilibrium for all the state variables in a system under a given model of population dynamics. Under specific dynamics, the existence of a feasible equilibrium is a necessary condition for species persistence regardless of whether the feasible equilibrium is dynamically stable or not. Thus, the size of the feasibility domain can also be used as an indicator of the tolerance of a community to random environmental variations. This has motivated a rich research agenda to estimate the feasibility domain of ecological communities. However, these methodologies typically assume that species interactions are static, or that input and output energy flows on each trophic level are unconstrained. Yet, this is different to how communities behave in nature. Here, we present a step-by-step quantitative guideline providing illustrative examples, computational code, and mathematical proofs to study systematically the feasibility domain of ecological communities under changes of interspecific interactions and subject to different constraints on the trophic energy flows. This guideline covers multi-trophic communities that can be formed by any type of interspecific interactions. Importantly, we show that the relative size of the feasibility domain can significantly change as a function of the biological information taken into consideration. We believe that the availability of these methods can allow us to increase our understanding about the limits at which ecological communities may no longer tolerate further environmental perturbations, and can facilitate a stronger integration of theoretical and empirical research.

1. Introduction

In ecological research, the feasibility of a community corresponds to the existence of an equilibrium point under which all species have positive abundances (Case, 2000; Hofbauer and Sigmund, 1998; MacArthur, 1970; Meszéna et al., 2006; Pimm, 1982; Roberts, 1974). Indeed, if one is interested in extant species, negative or zero abundances make no biological sense. Therefore, studying the feasibility of an ecological community is equal to determining whether under a given set of environmental conditions (abiotic and biotic) the dynamics of a community exhibits a feasible equilibrium point. That is, feasibility is a binary question: a community is feasible or not under a given set of environmental conditions. Nevertheless, one can also extend the study of feasibility by investigating the range of environmental conditions leading to a feasible community. This specific range of environmental conditions is known as the *feasibility domain* (Logofet, 1993). Thus, the size of the feasibility domain can be used as an indicator of the tolerance of a community to random environmental variations (Rohr et al., 2016; Saavedra et al., 2014). This has motivated a rich research agenda to estimate the feasibility of ecological communities in a systematic manner (Bastolla et al., 2009; Gilpin, 1975; Goh and Jennings, 1977; Grilli et al., 2017; Logofet, 1993; Meszéna et al., 2006; Rohr et al., 2014; Saavedra et al., 2017b; Stone, 2016; Vandermeer, 1975). Yet, it is still unclear how to integrate this systematic analysis with additional biological information, such as differences in energy flows across trophic levels or even changes in the structure of ecological communities.

Here, we present a step-by-step quantitative guideline to study the size of the feasibility domain of ecological communities under

* Corresponding author.
E-mail address: sersaa@mit.edu (S. Saavedra).
[1] ORCID 0000-0003-1768-363X

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changes of interspecific interactions and subject to different constraints on the trophic energy flows. This guideline covers multi-trophic communities that can be formed by any type of interspecific interactions. While our framework is based on the classic Lotka-Volterra (LV) dynamics (Page and Nowak, 2002), its advantage is that the structure and limits of the feasible regions of a large variety of ecological communities can be systematically studied using convex geometry and probability theory (Ball, 1997; Brondsted, 2012; Logofet, 1993; Rohr et al., 2014). Moreover, the applicability of this approach is not restricted to LV dynamics as long as the dynamics are topologically equivalent (Cenci and Saavedra, 2018).

This article is organized as follows. First, we discuss the mathematical definition, geometrical representation, and the probabilistic interpretation of the feasibility domain in multispecies communities characterized by LV dynamics. Then, we introduce new tools to incorporate both changes of species interactions and trophic energy constraints into the study of feasibility. After that we present an illustrative example to show how our tools can be applied to multi-trophic and changing communities. Finally, we discuss future promising avenues of research on feasibility. While we present an abridged guideline in the text, all the proofs can be found in the Appendixes A–E, and the computational codes in R Core Team (2017) is archived on Github.

2. Mathematical definition of feasibility

We start by assuming that the population dynamics in a multispecies community can be approximated by a LV system in the form

$$\frac{dN_i}{dt} = N_i\left(r_i + \sum_{j=1}^{S} a_{ij}N_j\right), \tag{1}$$

where the variable N_i denotes the abundance of species i, S is the number of species, the parameter r_i is the intrinsic growth rate of species i, and the parameter a_{ij} is the element (i, j) of the interaction matrix $\boldsymbol{A}$ and represents the effect of species j on species i (Case, 2000). Note that both the intrinsic growth rates and the elements of the interaction matrix can take either positive, negative, or zero values. We take into account only non-degenerate interaction matrices, i.e., $\det(\boldsymbol{A}) \neq 0$. This assumption is valid since it is extremely rare to have degenerate cases even under the setup of random matrix theory (Bruneau and Germinet, 2009).

Under the LV dynamics, the equilibrium state(s) of the population is(are) written as the vector $\boldsymbol{N}^*$, which corresponds to the state at which $dN_i/dt = 0$ for all species i. This equilibrium state(s) is(are) given by the solution(s) of the set of equations

$$N_i^*\left(r_i + \sum_{j=1}^{S} a_{ij}N_j^*\right) = 0. \tag{2}$$

The positivity of LV dynamics, i.e., species abundances will never be negative with strictly positive initial conditions, imposes two types of equilibria (Takeuchi, 1996). There can be either a border equilibrium, where at least a species goes extinct ($N_i^* = 0$ for some species i), or a *feasible* equilibrium (also known as *interior* equilibrium), where all species have positive abundances ($\boldsymbol{N}^* > 0$). If the feasible equilibrium exists is given by $\boldsymbol{N}^* = -\boldsymbol{A}^{-1} \cdot \boldsymbol{r}$. Moreover, one can mathematically prove that for a LV model, the existence of a feasible equilibrium point is a necessary condition for species persistence (and permanence), whether that feasible equilibrium is dynamically stable or not (Hofbauer and Sigmund, 1998).

The mathematical definition above reveals that feasibility depends strictly on the elements of both the interaction matrix $\boldsymbol{A}$ and the vector of intrinsic growth rates $\boldsymbol{r}$ (Song and Saavedra, 2018). This implies that, given an interaction matrix $\boldsymbol{A}$, only certain combinations of species-specific intrinsic growth rates can generate feasible equilibria, i.e., for which we have $-\boldsymbol{A}^{-1} \cdot \boldsymbol{r} > 0$. Following this rationale, studies have been systematically investigating the feasibility of ecological communities by looking at the range of parameter values of $\boldsymbol{r}$ as a function of a given interaction matrix $\boldsymbol{A}$ (Bastolla et al., 2009; Grilli et al., 2017; Logofet, 1993; Rohr et al., 2014; Saavedra et al., 2017b; Vandermeer, 1975). Importantly, since environmental conditions can be translated into the vital rates of species (Coulson et al., 2017; Levins, 1968; Meszéna et al., 2006; Roughgarden, 1975), the range of intrinsic growth rates leading to feasibility can represent a set of environmental variations tolerated by the community.

3. Geometrical representation of feasibility

As explained above, there is only a specific region of the parameter space of intrinsic growth rates that leads to feasible equilibria of a community given by an interaction matrix $\boldsymbol{A}$. This region is typically known as the *feasibility domain* (Logofet, 1993). Formally, this feasibility domain is described as

$$D_F(\boldsymbol{A}) = \{\boldsymbol{r} = N_1^*\boldsymbol{v}_1 + \cdots + N_S^*\boldsymbol{v}_S, \text{ with } N_1^* > 0, \ldots, N_n^* > 0\}, \tag{3}$$

where the vector $\boldsymbol{v}_j$ is the negative of the jth columns of the interaction matrix $\boldsymbol{A}$:

$$\boldsymbol{A} = \begin{bmatrix} a_{11} & \cdots & a_{1S} \\ \vdots & \ddots & \vdots \\ a_{S1} & \cdots & a_{SS} \end{bmatrix} = \begin{bmatrix} \vdots & \vdots & & \vdots \\ -\boldsymbol{v}_1 & -\boldsymbol{v}_2 & \ldots & -\boldsymbol{v}_S \\ \vdots & \vdots & & \vdots \end{bmatrix}. \tag{4}$$

In other terms, the vectors of intrinsic growth rates inside the feasibility domain are described by positive linear combinations of the S vectors given by the negative of each of the S columns of the interaction matrix (see Appendix A for further details).

This definition implies that the feasibility domain, $D_F(\boldsymbol{A})$, of an interaction matrix $\boldsymbol{A}$ can be geometrically represented as an algebraic cone (see Fig. 1a for a graphical illustration). An algebraic cone in $\mathbb{R}^S$ is defined as the space spanned by positive linear combinations of S linearly independent vectors. This cone is also referred in the mathematical literature as a *simplicial cone* (Ribando, 2006). For brevity, we will refer to it simply as a *cone*. Therefore, $\boldsymbol{v}_i$ can be defined as the i^{th} spanning vector of the feasible cone. This geometric property confirms, as we mentioned before, that the shape and size of the feasibility domain can be systematically investigated using convex geometry and probability theory (Ball, 1997; Brondsted, 2012; Logofet, 1993).

4. Probabilistic interpretation of feasibility

The definitions above allow us to quantify the size of the feasibility domain under LV dynamics by the solid angle of the cone generated by the interaction matrix $\mathbf{A}$ (see Fig. 1b for a graphical illustration). By normalizing the solid angle such that it is equal to one for the whole unit sphere in $\mathbb{R}^S$, the normalized solid angle $\Omega(\mathbf{A})$ is equal to the probability of sampling uniformly a vector of intrinsic growth rates on the unit sphere inside the feasibility domain. That is, the normalized solid angle is the proportion of the feasible parameter space inside the unit sphere. Formally, the normalized solid angle $\Omega(\mathbf{A})$ can be defined by the ratio of the following volumes:

$$\Omega(\boldsymbol{A}) = \frac{\text{vol}(D_F(\boldsymbol{A}) \cap \mathbb{B}^S)}{\text{vol}(\mathbb{B}^S)}, \tag{5}$$

where $\mathbb{B}^S$ is the closed unit ball in dimension S (Gourion and Seeger, 2010; Saavedra et al., 2016a). Note that the least upper bound of $\Omega(\boldsymbol{A})$ is 0.5, as the largest cone that can be generated by