



Microbial communities as dynamical systems

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Nowadays, microbial communities are frequently monitored over long periods of time and the interactions between their members are explored *in vitro*. This development has opened the way to apply mathematical models to characterize community structure and dynamics, to predict responses to perturbations and to explore general dynamical properties such as stability, alternative stable states and periodicity. Here, we highlight the role of dynamical systems theory in the exploration of microbial communities, with a special emphasis on the generalized Lotka–Volterra (gLV) equations. In particular, we discuss applications, assumptions and limitations of the gLV model, mention modifications to address these limitations and review stochastic extensions. The development of dynamical models, together with the generation of time series data, can improve the design and control of microbial communities.

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Introduction

Microbial communities are not static over time; abundances of members fluctuate from one measured time point to the next, sometimes drastically so. Longitudinal studies of host-associated and environmental microbiota have revealed several cases of complex dynamics, including periodicities, chaos and alternative stable states [1,2^{••}], as reviewed in [3]. Moreover, thanks to advances in

sequencing techniques, the number, length, and resolution of microbial community time series are all increasing rapidly; time series may cover a year or more, with monthly, weekly or even daily sampling intervals [1,4,5]. However, while we are gaining an ever more detailed picture of the composition and dynamics of many microbial communities, we still understand little of the rules that govern how these communities change over time.

Dynamical systems theory is a well-developed branch of mathematics that describes the change of complex systems such as microbial communities over time, and which is now increasingly applied to sequencing data [6–8]. In brief, the time development of a dynamical system, here the species composition of the community, can be described by a set of ordinary differential equations (ODEs) that encode the rules according to which the system changes. In some cases, prior biological knowledge of the system is sufficient to formulate these rules, while in others they can be derived from time series data. Dynamical systems theory highlights the conditions for the emergence of complex behavior and provides rigorous definitions of stability (see **Box 1**). The development and analyses of dynamical models thus allow microbial ecology to go beyond simple descriptions of community composition and statistical correlations, towards a better understanding of community dynamics.

Ordination plots visualize movement through community space

Microbial community time series are frequently visualized in ordination plots, where each sample is represented by a point and consecutive samples are connected by arrows (e.g. [9–11]). Ordination methods, such as Principal Coordinates Analysis (PCoA), display sample similarity computed from the high-dimensional species composition in a lower, typically two-dimensional space. Since microbial community time series often consist of rarefied counts or relative abundances and are therefore compositional, the sample similarity needs to be assessed by methods that have been designed for compositional data, such as the Aitchison distance [12]. Bray-Curtis dissimilarity is also a suitable option, yielding similar results for absolute and relative abundances [13]. Alternatively, the data can be transformed with a log ratio (e.g. the centered log ratio as in [14]).

In dynamical systems theory, the phase space represents all possible system states. A PCoA plot can be interpreted as a representation of the phase space. The points

Box 1 What does 'stability' mean?

Many theoretical works in ecology focus on 'stability'. However, the definition of this property varies from author to author. It is therefore important to distinguish them:

- **Linear asymptotic stability:** In the theory of non-linear dynamical systems, stability is determined by the behaviour of the system in response to a small, punctual perturbation in the variables (i.e. a change in abundance of some species in the present context) (see e.g. [31,65]). If, following the perturbation, the composition of a microbial community returns to its initial (steady) state, this state will be stable. In contrast, if the perturbation amplifies (meaning that the system diverges from its initial state), this state is unstable. In addition, stability is a local property: it does not imply anything about the long-term behaviour of the system and may not be valid for large perturbations.
- **Persistence/permanence:** These definitions of stability pertain to the long-term behaviour of a community. Both imply that a community will always maintain the species it started with, regardless of the size of the perturbation and even if it does not return to its original state [66], however, permanence is the stricter definition requiring that the boundary of the state space is a repeller: meaning if ever any species density approaches too close to zero, it will again begin to grow- and thus formally no species can ever go extinct [67].
- **Temporal stability and robustness:** Stability of an ecological system is sometimes assessed by the level of variability displayed by the community over time [68]. This variability may be attributed to stochasticity. A related definition refers to how much the composition of a system depends on small environmental changes, which are typically taken into account in the model parameters. If the community tends to remain constant over time or across parameter changes, it will be considered more stable. On the contrary, if the abundance of some species is sensitive to parameter changes, the system is considered less stable. This concept of stability is a measure of robustness — or resistance — to noise and to parameter values, and can be quantified by sensitivity analyses (parameters) or stochastic simulations (noise).
- **Structural stability:** A system is more structurally stable than another if its dynamical behaviour (e.g. the coexistence between several species) is maintained over a larger range of parameter values [69,70].

connected by arrows correspond to the trajectory of the system through the phase space (or community space, for simplicity). The community's movement through community space can be analyzed to test for instance whether the community moves randomly or tends towards a certain direction, or whether community composition changes more strongly during perturbation periods, implying larger jumps through community space. **Figure 1** illustrates trajectories for ocean and gut microbial communities, which provide examples of periodic behavior (**Figure 1a**) as well as the tendency to remain in the same region of the community space, suggesting the presence of a stable state (**Figure 1b**). While the gut community in **Figure 1b** returns to its stable state after a perturbation, thereby demonstrating resilience, a gut community from another person appears to switch to a second state upon perturbation (**Figure 1c**). While the phase space plot visualizes attractors such as stable states, alternative plots such as recurrence plots and periodograms serve to explore other aspects of the behavior of dynamical systems, such as periodicity.

Recently, the Anna Karenina principle (AKP) of dysbiotic communities has been put forward [15,16^{*}], which states that dysbiotic communities tend to exhibit greater inter-subject variability than the 'reference' community in healthy hosts. The observation that perturbation periods contain larger jumps than are present before the perturbation (**Figure 1d**) suggests a dynamical formulation of the AKP, where perturbed communities tend to vary more strongly over time than healthy communities. Although experimental evidence supports this dynamic version of the AKP [17^{*}], it remains to be tested systematically.

What can we learn from community models?

Mathematical approaches provide the means for systematic quantitative characterization of observed patterns and their underlying mechanisms, and have a long-standing history in ecology (e.g. [18,19]). While a number of models have been proposed in microbial community ecology (reviewed e.g. in [20]), we will discuss in particular the generalized Lotka–Volterra (gLV) model, since it has become one of the most popular microbial community models to date (e.g. [6,21]).

The gLV model is a classical ordinary differential equations (ODEs) model that characterizes the dynamics of a multi-species system. It describes the change over time of a population of N species as a function of their intrinsic growth rates and the interactions between species (see the supplement). Interactions can be unidirectional (species i affects species j , but not the other way round; e.g. commensalism) or reciprocal (species i affects species j and vice versa; e.g. competition and parasitism). Together, these interactions encode the community network. Thus, the gLV model can capture a number of commonly encountered network structures, including food chains, modularity, scale-freeness and small-world networks (e.g. in [22,23]).

The utility of the gLV model for studying microbial communities is twofold: it offers a convenient tool to interpret existing empirical data, and provides a framework to make broader predictions about the factors that govern microbial communities' stability and dynamics. An increasing number of methods have been developed with which to fit gLV models to large-scale longitudinal (and in certain cases, cross-sectional) data [7,8,24,25]. In these studies, observed data are used to assign values to the intrinsic growth rates and interspecies interactions associated with each member of a microbial community. Thus, one can determine not only how each species' abundance changes over time, but how this change is influenced by each of the other members of the community. Through learning these parameters, researchers have been able to identify members of microbial communities that play important roles both for broad scale community properties (e.g. keystone species that influence many other community members [7]) and for

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