

Non-equilibrium dynamics of microbial ecosystems

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Understanding the ecological forces that shape microbial communities is a fundamental problem in ecology. In this context, macroecology has established itself as an important top-down approach to connect such mechanisms with the statistical patterns of coexistence, abundance and diversity. In this work, we unveil some of the mechanistic consequences of the Ecological Forces upon the emergence of macroecological patterns. For this purpose, we advanced a population dynamics model which explicitly takes into account microbial interactions and resources fluctuations:

$$\dot{x}_i = \frac{x_i}{\tau_i} \left(1 - \frac{x_i}{K_i} + \sum_{j \neq i}^S a_{ij} x_j \right) + x_i \xi_i(t) \quad (1)$$

where x_i is the abundance of species i , S is the total number of species, τ_i is the time scale of basal population growth, K_i is the maximum carrying capacity, $(a_{ij}) = \hat{A}$ is the Lotka-Volterra interaction matrix and ξ_i is a zero-mean Gaussian noise with correlations $\langle \xi_i(t) \xi_j(t') \rangle = w_{ij} \delta(t-t')$ –aimed to describe environmental fluctuations–.

Experimental evidence suggests modelling *biotic* interactions through matrix \hat{A} , which describes a weighted and directed network whose nodes represent species and edges represent interactions strength and direction. On the other hand, *abiotic* factors are encoded in the diffusion matrix, $\hat{D} = (w_{ij} x_i x_j)$. When $i \neq j$, w_{ij} describes the resource preference of the pair of species (i, j) , thus if $w_{ij} > 0$ species have a preference for the same resources/environmental conditions, whereas they have an opposite preference if $w_{ij} < 0$.

Both types of ecological forces have gathered significant attention in recent works [1, 2, 3]. Direct species interactions \hat{A} , for instance, play a pivotal role in reproducing abundance correlations [1], while the response of species to environmental fluctuations, \hat{D} , can yield correlations based on phylogenetic closeness [2]. However, the dynamics of ecosystems remains understudied when both types of interactions coexist. In our work, we unveil the intricate interplay between biotic and abiotic forces, elucidating non-trivial effects that elude comprehension through the analysis of each force type in isolation. For instance, the single-species patterns [3] are independent of resource fluctuations when considered alone but produce alterations when considered at the same time with interactions. Even though, closed analytical solutions of equation (1) can not be obtained, it can be solved using a mean field approximation, which is accurate

enough for a wide range of parameters.

Finally, the interplay of ecological forces maintains the ecosystem out of thermodynamic equilibrium, which we elucidate through the synthesis of four distinct dynamical forces (see Fig. 1 for a two-dimensional example). Equilibrium (detailed balance is fulfilled) is only achieved when the magnitudes of biotic and abiotic factors are equal yet opposing in direction. Importantly, we establish that under such a regime, model equation (1) is equivalent to the "stochastic consumer-resource" model, a well-established framework widely employed in the study of microbial ecosystems. Our findings demonstrate that our proposed model serves as a concrete instantiating of the established one, providing further validation and applicability to the field.

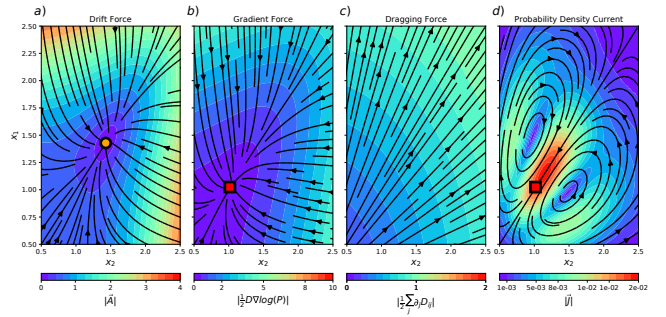


Fig. 1. Non-equilibrium dynamics of a two species ecosystems. The existence of a non-vanishing probability flux at steady state, panel **d**), indicates that the detailed balance is broken. The driving force of equation (1), panel **a**), can be decomposed into a part that is the negative gradient of a non-equilibrium potential, panels **b**) and **c**), and a part involving a rotational curl, panel **d**).

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- [1] J. Camacho-Mateu, A. Lampo, M. Sireci, MA. Muñoz and J. Cuesta, *Species interactions reproduce abundance correlations patterns in microbial communities*, arXiv:2305.19154.
- [2] M. Sireci, MA. Muñoz, J. Grilli, *Environmental fluctuations explain the universal decay of species-abundance correlations with phylogenetic distance*. *bioRxiv*, 2022-07.
- [3] J. Grilli, *Macroecological laws describe variation and diversity in microbial communities*. *Nature communications*, 11(1), 4743.