Lotka-Volterra dynamics of projected Consumer-Resource networks

Pablo Lechón Alonso

June 2021

Abstract

The most widespread approach to model microbial communities is through consumer resource (CR) models, but recent empirically supported extensions render them analytically intractable. To sidestep this problem a separation of timescales between resource and population dynamics it is often assumed. However, the suitability of this simplification lacks rigorous support. Here, I shade light on this question by simulating the dynamics of a CR model with cross-feeding and its equivalent Generalized Lotka-Volterra (GLV) model, obtained by projecting the bipartite consumer resource network onto the unipartite interactions matrix A. Overall I find that the information lost during the projection process has an effect that makes the dynamics of the GLV and CR models not equivalent. Nonetheless, in a sub-region of the explored parameter space, where all resources are homogeneously distributed across the community, the two models display similar qualitative dynamics at equilibrium. My findings cast doubt on many previous results that indirectly make use of some sort of network projection when assuming the separation of time scales, and also suggest that when this approximation is valid, simpler modeling approaches are possible, allowing theoreticians to perform deep mathematical explorations of these complex microbial systems.

1 Introduction

Microbial communities are widespread throughout our planet (Fierer & Jackson 2006), from the human gut to the deep ocean, and play a critical role in natural processes ranging from animal development and host health (Huttenhower et al. 2012, McFall-Ngai et al. 2013) to biogeochemical cycles (Falkowski et al. 2008). These communities are very complex, typically harboring hundreds of species (Gilbert et al. 2014), making them hard to characterize. Recently, DNA sequencing has allowed a high-resolution mapping of these communities, opening a niche for theoreticians and experimentalists to collaboratively decipher their complexity and assembly (Costello et al. 2012, Friedman et al. 2017, Goldford et al. 2018, Goyal & Maslov 2018, Marsland et al. 2019, Vila et al. 2019, Estrela et al. 2020, Coyte et al. 2021).

The most widespread approach to model these communities is through consumer resource (CR) models, which origin dates back to the work of Macarthur & Levins (1967). Recently, they have been extended to include cross-feeding, in order to model the fact that microbial species perform both consumption, and also release to the environment the waste by-products of their metabolism Goldford et al. (2018). However, this extension renders consumer-resource models analytically intractable, since one cannot even find a closed expression for the equilibrium of the system. Different simplifications have been explored that allow for an analytical approach without severely compromising the reality of the model. The most popular choice to simplify the dynamics is to assume a separation of timescales be-

tween resource and population dynamics, so that one can solve for the equilibrium of resources separately, and then insert the solution for resources into the population equation, and solve it analytically (Tikhonov 2016, Pacciani-Mori et al. 2020, Fant et al. 2021). Despite numerous interesting results stemming from this approximation, the question remains as to how appropriate it is, and how much of the realism provided by this modeling framework is being lost when making these assumptions. Specifically, one could argue that setting the resources to their equilibrium value from the start of the dynamics, is to essentially eliminate the effect of the resources, making them just a static environment property that contributes to determining the growth rate and interactions of each species. These two items are precisely the only pieces of information required to integrate the Generalized Lotka-Volterra (GLV) equations. Thus, one could use the information in the resource preferences of the consumers in the microbial community to compute an estimate of the species growth rates and construct a matrix of pairwise interactions, defining the GLV-equivalent to the CR model.

In this work, I explore the dynamics of a GLV model where its interaction matrix A is given by the projection of the bipartite network obtained from the CR model, under different network projections, interaction type, and strengths, and community-environment complexity values. I find that, in general, the GLV-equivalent does not reproduce dynamics qualitatively similar to those stemming from its parent CR model. However, within a region of the explored parameter space (possibly feasible from an ex-

perimental standpoint), the two models, CR and its GLV-equivalent do exhibit qualitatively similar dynamics, validating the popular time scale separation assumption, and opening the door for simpler ways to model microbial communities.

2 Mathematical models

I use a mathematical model based on Marsland et al. Marsland et al. (2019) for the microbial consumer-resource dynamics:

$$
\frac{dn_\alpha}{dt} = g_\alpha n_\alpha \left((1-l) \sum_j c_{\alpha j} R_j - z_\alpha \right),
$$
$$
\frac{dR_j}{dt} = \kappa_j - \sum_\alpha n_\alpha c_{\alpha j} R_j + l \sum_{\alpha k} n_\alpha D_{kj} c_{\alpha k} R_k. \tag{1}
$$

Here, n_α ($\alpha = 1, \ldots, s$) and R_j ($j = 1, \ldots, m$) are the biomass abundance of the αth microbial (e.g., bacterial) species and the concentration of the jth resource (e.g., carbon source). The growth of species α is determined by the resources it harvests minus the cost of maintenance (two terms in the brackets). Resource uptake depends on the resource concentration in the environment R_j, and whether or not the species α uses resource j ($c_{\alpha j} = 1$ or $c_{\alpha j} = 0$, respectively). The leakage term l determines the proportion of this uptake that is released back into the environment as metabolic by-products, with the remainder ($1-l$) being allocated to growth. The maintenance cost term, z_α, is dependent on the number of resources that the αth species consumes, and is given by the expression:

$$
z_\alpha = \chi_0 (1 + \epsilon) \sum_j c_{\alpha j}, \tag{2}
$$

where χ_0 is the average cost of being able to consume a given resource, the summation represents the total number of resources that species α is able to process, and ϵ is a random fluctuation sampled from a truncated (so that $z_\alpha > 0$) normal distribution. Eq 2 ensures that neither generalists nor specialists are systematically favored during the community assembly by imposing a greater cost on species that consume a wider range of resources. The uptake that remains after subtracting this maintenance is transformed into biomass with a proportionality constant of g_α, the value of which does not affect the results presented here.

The change in the concentration of resources in the environmental pool is determined by three terms. The first term represents the external supply κ_j, which gives the rate at which the jth resource enters the system. The second term is the uptake of the jth resource from the environment, summed across all s consumers in the system and the third term represents resources entering the environmental pool via leakage of metabolic by-products. By-product leakage is determined by the metabolic matrix D (or

the "stoichiometric" matrix; Marsland et al. (2019)), with the jk^{th} element representing the leaked proportion of resource j that is transformed into resource k. Due to conservation of energy, D is, by definition, a row stochastic matrix, meaning that its rows sum to 1.

The above model entails the following assumptions: (i) all resources contain the same amount of energy (taken to be 1 for simplicity), (ii) a type I functional response, (iii) binary consumer preferences, (iv) a shared core metabolism encoded in D, (v) a common leakage fractions for all species and resources, and (vi) a complex environment where all resources are externally supplied in equal amounts.

The Generalized Lotka-Volterra model can be written in compact form as:

$$
\frac{dn}{dt} = \mathcal{D}(n)(r + An) \tag{3}
$$

where n is a (column) vector of length s containing the densities of all populations $1, \ldots, n$ at time t, r is a vector of "intrinsic growth rates" (or death rates, when negative), measuring the growth (decline) of population α when grown alone at low density, and they are determined by the consumer preferences as:

$$
r_n = (1-l) \sum_j c_{\alpha j} R_j^0 - z_\alpha, \tag{4}
$$

where R_j^0 is the initial resource concentration. The matrix A is a $s \times s$ matrix of interaction coefficients, which elements are given by expressions derived in the next section. I use $\mathcal{D}(n)$ to denote the diagonal matrix with n on the diagonal.

3 Network projection

Bipartite network projection is an extensively used method for compressing information about bipartite networks (consumer-resource network in our case). Since the one-mode projection is always less informative than the original bipartite graph, an appropriate method for weighting network connections is often required Zhou et al. (2007). In our case, I weight the links between species in the CR model by calculating pairwise competition ($\mathcal{C}$) and facilitation ($\mathcal{F}$) estimates, which I now define.

In the system described by Eqs 1, facilitation occurs when a species leaks metabolic by-products that are used by another species. I compute the strengths of facilitation between individual species pairs $\alpha \to \beta$ as:

$$
F_{\alpha\beta} = l \sum_{jk} \tilde{\kappa}_j c_{\alpha j} D_{jk} c_{\beta k}, \tag{5}
$$

where l is the strength of cooperative links, and the term $c_{\alpha j} D_{jk} c_{\beta k}$ represents the necessary condition to establish a cooperative link.

Competition for resources exists because of the overlap in resource preferences (the $c_{\alpha j}$'s) between species. The realized strength of competition between species depends on the resource environment

they experience, which is made up of two sources; the externally supplied resources, and the metabolic by-products generated by the community. Similar to facilitation, I develop new metrics of pairwise competition strengths that account for each of these sources: $(C_a)_{\alpha\beta}$ measures the level of competition between species pair (α, β) for externally supplied resources, and $(C_b)_{\alpha\beta}$ the level of competition for resources that have been leaked by species across the community.

I define the competition for externally supplied (abiotically-generated) resources $(C_a)_{\alpha\beta}$ to be

$$(C_a)_{\alpha\beta} = (1 - l) \sum_k \tilde{\kappa}_k c_{\alpha k} c_{\beta k}.$$

That is, intrinsic competition between the species pair is quantified by their common resource preferences through the scalar product of their preference vectors. Interaction strength is determined by the fraction of externally supplied resources that is effectively consumed, $1 - l$, and the factor $\tilde{\kappa}_k$ accounts for possible differences in external supply rate between resources.

Competition for resources leaked as metabolic by-products (biotically-generated resources), and is written as

$$(C_b)_{\alpha\beta} = l \sum_{jk} \tilde{\kappa}_j D_{jk} \left(c_{\alpha j} + c_{\beta j} \right) c_{\alpha k} c_{\beta k}.$$

Here, l is the strength of competition on leaked resources, and the product $D_{jk}(c_{\alpha j} + c_{\beta j}) c_{\alpha k} c_{\beta k}$ represents the necessary conditions to have effective competition for the kth leaked resource.

Finally, the total competition is calculated as

$$C_{\alpha\beta} = (C_a)_{\alpha\beta} + (C_b)_{\alpha\beta} \tag{6}$$

4 Community assembly

Using the scipy package of python 3, I numerically simulate the dynamics of each parent community according to Eqs 1 and 3 until steady state is reached. I compute the community interaction matrix A of the GLV model under two different projections. First, including the effects of cross-feeding (Fig 1A), and second, without them (Fig 1B), such that

$$A = F_{\alpha\beta} - C_{\alpha\beta} \qquad \& \qquad A = -C_{\alpha\beta} \tag{7}$$

For each scenario, I assemble communities for all possible combinations of leakage (18 values evenly spaced between 0.01 and 0.95) and complexity (10 values evenly spaced between 10 and 65) values. I define complexity as the square root of the product of the number of species present in the chemostat, and the number of existing resources, that is, $\sqrt{ms}$. Throughout all performed simulations, I imposed the constraint $m = s$ for simplicity. Additionally, within each leakage-complexity pair, I perform 250 replicates of a random assembly.

5 Results

First, I simulate the dynamics of both models (the CR and its GLV equivalent) assuming that the cross-feeding of the consumer resource model has an effect on the pairwise interactions between species (Fig 1A). I observe that there is a considerable portion of cases where the GLV model does not converge, particularly, under a certain threshold where leakage and/or complexity are sufficiently low and/or high, respectively. However, for high values of leakage and/or low values of complexity, the GLV model converges widely. Within the convergence region, a pattern can be mildly appreciated where higher values of correlation show when leakage is maximum and complexity is minimum.

Second, I simulate the dynamics of both models assuming that the cross-feeding of the consumer resource model does not have an effect on the pairwise interactions between species (Fig 1B). Expectedly, the convergence problems disappear in this case, consequent with the circular law stemming from random matrix theory (if the center of the circle is displaced to the negative, it is less likely that at least one eigenvalue will be positive). Surprisingly, when we discard the effects of facilitation, the previous pattern becomes more acute, clearly showing that maximum correlation between the average abundances under each type of dynamics is reached when leakage is maximum and complexity is minimum.

6 Discussion

In this work, I simulated the dynamics of a CR model with cross-feeding and its equivalent GLV obtained by projecting the bipartite consumer resource network onto the unipartite interactions matrix A. Under what conditions the GLV behaves qualitatively the same as the dynamics of a CR model with cross-feeding? The short answer is: when the system is not too complex (that is, not many resources and species are present) and leakage is high. In the following, I expand on the interpretation of these findings.

The two models seem to have closer behavior when the projection of the bipartite network onto the unipartite one is performed without accounting for the effects of facilitation. This could be due to the fact that the GLV model is mainly a competitive model, and has not been conceived to naturally incorporate cooperative forces. In fact, these are not explicitly included in the model, but instead indirectly incorporated by "damping" the competition coefficients between cooperative species pairs. Interestingly, however, the two models behave more closely at equilibrium when the effects of cross-feeding (and therefore, of cooperation) are strongest, that is, at the highest values of leakage. Why an inherently competitive model such as the GLV resembles the CR-cross-feeding model most accurately within the regime where cooperation is maximized?
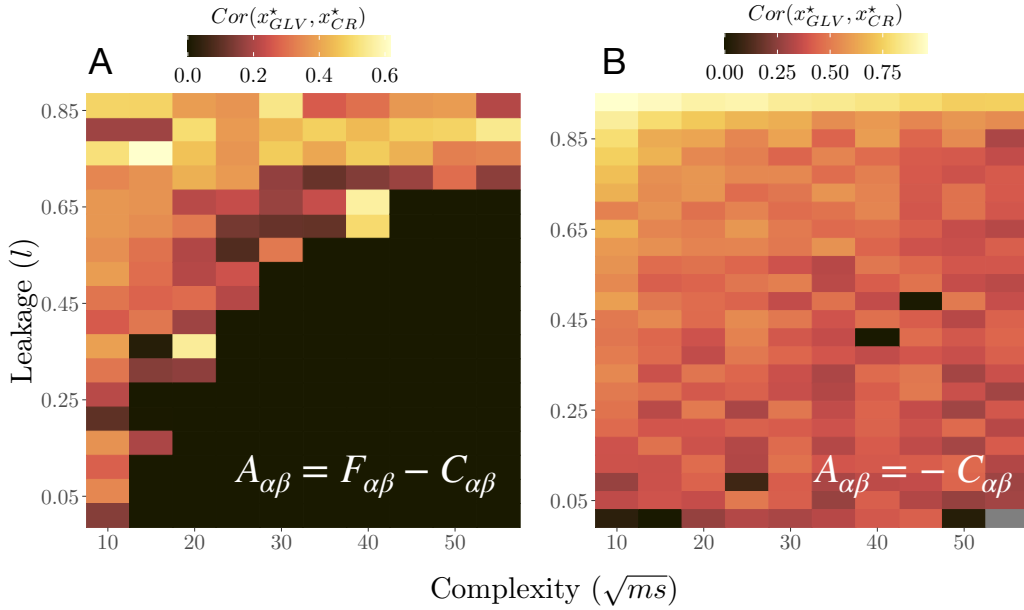
Figure 1: Correlation between average abundances in GLV and CR at equilibrium, as a function of leakage (l) and complexity ($\sqrt{ms}$). In **(A)** Projection is performed accounting for the effects of facilitation, and in **(B)** the effects of facilitation are ignored. Excepting the fact that the GLV under the projection without facilitation exhibits more divergent dynamics (black rectangles), both projections capture the same pattern: maximum correlation between model dynamics is reached at high leakage and low complexity.

There are several reasons that might be contributing to this finding. An important caveat to keep in mind is that the fact that average abundances at equilibrium behave the same does not mean that the individual species abundances between the two models are correlated. Instead, it suggests that the ecosystem overall biomass (ecosystem function) reached at equilibrium behaves similarly for both models. This could be due to the fact that at high leakage, the strong cooperative links are able to counter the effects of competition by making all resources more evenly available across the community. Another possibility is that higher-order interactions, which become more influential as the system becomes more complex due to the dense metabolic cross-feeding network, are affecting the dynamics in a way that is lost when we project the network. Finally, note that projecting a bipartite network retains information about the strength and sign of the interacting species, but not about the resources through which these interactions are taking place. When leakage is high, all the resources are being equally redistributed across the community, because the topology of the metabolism (matrix D) is very uniform in our parametrization. This causes the resources to become neutral (all are virtually equivalent). Since there is no information distinguishing each resource, nothing is to be lost when projecting the network, and both systems behave the same. On the other hand, when leakage decreases, not all resources are equivalent. Some are consumed more than others due to irregular consumer preferences, and the low leakage fraction does not homogenize the resource profile. When we perform the projection, this information is lost causing

the GLV model to behave differently than its CR counterpart.

Overall I find that the information lost during the projection process has an effect, in general, on the dynamics of the GLV model, rendering it not equivalent to a CR model. This result casts doubt on many previous results that indirectly make use of some sort of network projection when they assume the separation of timescales between resources and population dynamics. However, in a sub-region of the explored parameter space (roughly where leakage is high), all resources become essentially equivalent, since they are homogeneously distributed across the community through the dense and uniform metabolic cross-feeding matrix D. In this case, the two models display similar qualitative dynamics at equilibrium, because the information that one would lose when projecting was never there in the first place. It remains to be seen what situations in the natural world would put us in a regime of high leakage and low complexity, but in the case that they exist, we would expect simpler modeling approaches, like the one shown here, to be possible, allowing theoreticians to perform deep mathematical explorations of the complex microbial systems.

Supplementary material

All the code used to perform the simulations, analyze the results, and plot the figures can be found at the GitHub repository: `https://github.com/pablolich/ECEV44500_network_project`.

References

Costello, E. K., Stagaman, K., Dethlefsen, L., Bohannan, B. J. & Relman, D. A. (2012), 'The application of ecological theory toward an understanding of the human microbiome', *Science* **336**(6086), 1255–1262.

Coyte, K. Z., Rao, C., Rakoff-nahoum, S. & Foster, K. R. (2021), 'Ecological rules for the assembly of microbiome communities', **19**(2), e3001116.
URL: *http://dx.doi.org/10.1371/journal.pbio.3001116*

Estrela, S., Vila, J. C., Lu, N., Bajic, D., Rebolleda-Gomez, M., Chang, C. Y. & Sanchez, A. (2020), 'Metabolic rules of microbial community assembly'.

Falkowski, P. G., Fenchel, T. & Delong, E. F. (2008), 'The microbial engines that drive earth's biogeochemical cycles', *Science* **320**(5879), 1034–1039.

Fant, L., Macocco, I. & Grilli, J. (2021), 'Eco-evolutionary dynamics lead to functionally robust and redundant communities', *bioRxiv* p. 2021.04.02.438173.
URL: *http://biorxiv.org/content/early/2021/04/02/2021.04.02.438173.abstract*

Fierer, N. & Jackson, R. B. (2006), 'The diversity and biogeography of soil bacterial communities', *Proceedings of the National Academy of Sciences of the United States of America* **103**(3), 626–631.

Friedman, J., Higgins, L. M. & Gore, J. (2017), 'Community structure follows simple assembly rules in microbial microcosms', *Nature Ecology and Evolution* **1**(5), 41559–017.

Gilbert, J. A., Jansson, J. K. & Knight, R. (2014), 'The Earth Microbiome project: Successes and aspirations', *BMC Biology* **12**(69), 12915–014.

Goldford, J. E., Lu, N., Bajić, D., Estrela, S., Tikhonov, M., Sanchez-Gorostiaga, A., Segrè, D., Mehta, P. & Sanchez, A. (2018), 'Emergent simplicity in microbial community assembly', *Science* **361**(6401), 469–474.

Goyal, A. & Maslov, S. (2018), 'Diversity, Stability, and Reproducibility in Stochastically Assembled Microbial Ecosystems', *Physical Review Letters* **120**(15), 158102. doi: 10.1103/PhysRevLett.120.158102.

Huttenhower, C., Gevers, D., Knight, R. & Al., E. (2012), 'Structure, function and diversity of the healthy human microbiome', *Nature* **486**(7402), 207–214.

Macarthur, R. & Levins, R. (1967), 'The Limiting Similarity , Convergence , and Divergence of Coexisting Species', **101**(921), 377–385.

Marsland, R., Cui, W., Goldford, J., Sanchez, A., Korolev, K. & Mehta, P. (2019), 'Available energy fluxes drive a transition in the diversity, stability, and functional structure of microbial communities', *PLoS Computational Biology* **15**(2), e1006793. doi: 10.1371/journal.pcbi.1006793.

McFall-Ngai, M., Hadfield, M. G., Bosch, T. C., Carey, H. V., Domazet-Lošo, T., Douglas, A. E., Dubilier, N., Eberl, G., Fukami, T., Gilbert, S. F., Hentschel, U., King, N., Kjelleberg, S., Knoll, A. H., Kremer, N., Mazmanian, S. K., Metcalf, J. L., Nealson, K., Pierce, N. E., Rawls, J. F., Reid, A., Ruby, E. G., Rumpho, M., Sanders, J. G., Tautz, D. & Wernegreen, J. J. (2013), 'Animals in a bacterial world, a new imperative for the life sciences', *Proceedings of the National Academy of Sciences of the United States of America* **110**(9), 3229–3236.

Pacciani-Mori, L., Giometto, A., Suweis, S. & Maritan, A. (2020), 'Dynamic metabolic adaptation can promote species coexistence in competitive microbial communities', *PLoS Computational Biology* **16**(5), 1–18.
URL: *http://dx.doi.org/10.1371/journal.pcbi.1007896*

Tikhonov, M. (2016), 'Community-level cohesion without cooperation', *eLife* **5**, e15747. doi: 10.7554/eLife.15747.

Vila, J. C., Jones, M. L., Patel, M., Bell, T. & Rosindell, J. (2019), 'Uncovering the rules of microbial community invasions', *Nature Ecology and Evolution* **3**(8), 1162–1171.

Zhou, T., Ren, J., Medo, M. & Zhang, Y.-C. (2007), 'Bipartite network projection and personal recommendation Tao', *Physical Review E* **76**(4), 046115.