Luis F. Jover, School of Physics, Georgia Institute of Technology, Atlanta, GA, USA
Michael H. Cortez, School of Mathematics & School of Biology, Georgia Institute of Technology, Atlanta, GA, USA
Joshua S. Weitz, School of Biology & School of Physics, Georgia Institute of Technology, Atlanta, GA, USA

Mechanisms for Coexistence in Host-Phage Systems with Nested Interaction Networks

Viruses are ubiquitous in nature and the most abundant biological life-form on Earth. Globally, their estimated abundance is 10^{30} particles. Viruses have profound ecological effects; by infecting, exploiting and sometimes killing their hosts, they affect the dynamics and composition of all types of biological communities. They are particularly relevant in the study of aquatic bacterial communities where they are thought to be responsible for 20-40% of bacterial mortality. In these communities different host species and their viral pathogens (i.e. phages) coexist, creating complex interaction networks where different viral strains have overlapping host ranges. A recent meta analysis of host-phage interaction networks revealed that such networks tend to be nested [1]. In nested systems, there is a hierarchy for who can infect whom. In particular, the specialist virus can infect the most permissive host, whereas the host that is most difficult to infect gets infected by the more generalist virus. The mechanisms through which viral strains with overlapping host ranges coexist are not well understood. For example, the emergence of nestedness may reflect important ecological principles at work that have been overlooked in the past where viral strains were often assumed to only infect a single host. In this study we ask if the property of nestedness might yield insight into mechanisms allowing coexistence in multi-strain host-phage systems.

We present our analysis of a multi-stain host-phage system using a modified Lotka-Volterra (LV) framework. LV models have been used in the study of phage-host interactions[2,3]. Here, we modify the typical LV framework to explicitly incorporate the interaction among N viral strains and N host strains. We begin by assuming that the N-by-N interaction matrix is perfectly nested. We solve the model for conditions of coexistence at equilibrium and assess the possibility of coexistence for systems starting away from equilibrium by looking at the stability of the boundary equilibria. We validate our results using numerical simulations and show how coexistence can be obtained via different types of dynamics which can be different from a locally stable steady state.

We find two general requirements for the coexistence of viral and host strains in perfectly nested systems. First, there should exist a trade-off in the viral strains between life-history traits and host range. These viral traits include: adsorption rate, burst size, and death rate. Second, there should exist a trade-off in the host strains between immunity and growth rate. We find that properties of these trade-offs can predict relative densities of the viral and host strains. Importantly, we find that the strength of the trade-off, as measured by its curvature in terms of species rank, determines the relative densities of viruses and hosts. For example, specialist viruses may have higher abundances than generalist viruses, or vice versa, depending on the relationship between life history traits and host range. We also study systems that are not perfectly nested. In these systems, we find that species can coexist if the viral host ranges are sufficiently different (specifically, if the interaction matrix is invertible). For non-invertible interaction matrices (e.g. complete overlap in host range) coexistence can still be achieved by quantitative changes in the strength of the interactions. Finally, we discuss how our analysis provide insights in the more general endeavor of understanding the relationship between the structure of networks and the properties of ecological communities such as biodiversity and stability. Specifically, we show that it is important to consider the constraints that the structure of interaction networks imposes on the different interaction parameters.

References
1. Flores C.O., Meyer J.R., Valverde S. ,Farr L. ,Weitz J.S., Statistical structure of host phage interactions. Proc. Natl. Acad. Sci., 108(28):E288-E297, Jul 2011.
2. Sivan P.,Gabay C., Kishony R., Oppenheim A., Balaban N.Q., Nongenetic individuality in the host-phage interaction. PLoS Biology, 6(5):957-964, May 2008.
3. Thingtad T.F., Elements of a theory for the mechanisms controlling abundance, diversity, and biogeochemical role of lytic bacterial viruses in aquatic systems. Limnology and Oceanography, 45(6):1320-1328, Sep 2008.