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Ecology and evolution in microbial systems: the generation and maintenance of diversity in phage–host interactions

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Abstract

Insights gained from studying the interactions between viruses and bacteria have important implications for the ecology and evolution of virus–host interactions in many environments and for pathogen–host and predator–prey interactions in general. Here, we focus on the generation and maintenance of diversity, highlighting recent laboratory and field experiments with microorganisms.

Keywords: Virus; Bacteriophage; Microbial diversity; Microbial interactions; Coevolution

1. Introduction

Microbial ecology is in a renaissance of sorts, with microbiologists increasingly using ecological and evolutionary theory to inform fundamental questions about microbes, and ecologists and evolutionary biologists increasingly using controlled experimental systems containing viruses and bacteria to test theory. Although the use of microbial experimental systems is not new (in fact, some of the earliest experiments date back to 1887, when Rev. W.D. Dallinger conducted long-term evolutionary experiments with protists and observed that specialization in one environment can yield a ‘‘cost’’ of adaptation [14]), communication between microbiologists, ecologists and evolutionary biologists has become commonplace.

The use of microbial experimental systems in the laboratory offers a number of advantages to the biologist seeking to investigate the theoretical predictions of ecology and evolution. The small size and short generation time of most microorganisms facilitate experiments across a wide range of spatial and temporal scales. The most commonly used microorganisms are well-characterized genetically and physiologically. Furthermore, populations can be genetically manipulated with relative ease. Communities of microorganisms can be stored in a state of ‘‘suspended animation’’ and can be further investigated post hoc. These features enable researchers to untangle the complexity of the natural world and investigate the mechanisms underlying ecology and evolution in relatively simple, controlled and replicated systems [33].

The striking abundance of viruses and bacteria in nature has also prompted many questions about their ecology and evolution in situ [50]. Microbes are mediators of many important ecosystems and industrial processes, and some microbes are pathogens. In a recent discussion of the role of ecological theory in microbial ecology, Prosser et al. [50] argue that the ecology of microorganisms is ‘‘one of the most compelling intellectual changes facing contemporary ecology’’. Advances in molecular techniques and statistical methods have enabled scientists to study the diversity of bacteria and viruses in marine systems, agricultural plots, deserts and other environments worldwide. Powerful molecular and physiological techniques offer the exciting ability to test the real generality of ecological and evolutionary principles.

One of the most fundamental goals in ecology and evolution is understanding the generation and maintenance of

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diversity. There is a rich theoretical literature on biological diversity, but experimental studies of the plausibility of various related hypotheses have lagged behind the development of theory, primarily because of the inherent difficulty of addressing these questions in field systems and with long-lived organisms. The generation and maintenance of diversity depend on several critical factors including evolution, adaptation, environmental heterogeneity and trophic interactions. Many of these factors have been studied in microorganisms in the laboratory and in the field. Here, we review recent advances from laboratory microbial experimental systems and from field studies of microorganisms that address the generation and maintenance of diversity. We focus on studies of the interactions between viruses and bacteria in the laboratory that have been used to inform ecological and evolutionary theory and studies of viruses and bacteria in the field that use ecological and evolutionary theory to elucidate microbial interactions.

2. The process of adaptation

Adaptation is central to the generation of phenotypic diversity and understanding this process has been a major focus of evolutionary biology since the time of Darwin [43]. Adaptation occurs through the spread and substitution of mutations that improve the overall fitness of an organism in its environment [19]. To formally address hypotheses about adaptation and the process of evolution requires controlled experiments. Some of the most compelling studies of evolution utilize laboratory experimental systems and many of these involve viruses. Such experiments not only elucidate the process evolution. They also provide insights about the forces of selection that underlie the observed current distributions of organisms in nature.

2.1. The costs of adaptation and life history trade-offs

Most models of adaptation assume that organisms face trade-offs in fitness across different environments. Without such trade-offs, a single superorganism, often referred to as the ‘‘Darwinian demon’’, would prevail in all environments. Identifying and measuring such trade-offs, which are difficult in long-lived macroorganisms, have been the subject of several microbial experiments with viruses. For example, Chao et al. [12] demonstrated that coevolution between phage T7 and *E. coli* B yielded phage-resistant strains of bacteria and subsequent host-range variants of T7 that could infect these strains. Competition assays revealed that the evolved host-range phage was less fit on the ancestral host than the wild-type phage.

Viruses display a high degree of variation in virulence resulting from the need to adapt to dynamic host populations. A key trade-off thought to underlie the evolution of virulence is that between levels of virulence and reproduction. Evolution experiments with viruses have provided a fertile testing ground for understanding such trade-offs in life history characteristics, which are thought to maintain diversity.

In an experiment with the bacteriophage f1, Messenger and colleagues [46] varied selection against virulence while periodically requiring phage transmission to new hosts. The phage f1 can be transmitted both horizontally and vertically; thus each episode of vertical transmission (which selects for low virulence) was followed by an episode of horizontal transmission (which selects for high fecundity). The experimental design varied the relative intensity of selection against virulence, but maintained selection for some level of reproduction. Lines with higher enforced transmission evolved higher virulence and higher rates of viral production (Fig. 1), which support the predictions of the trade-off model for the evolution of virulence [46].

The trade-off between reproductive output and virulence is intimately linked to the relationship between fecundity and generation time. A number of studies with phage have focused on the evolution of lysis timing (i.e., generation time) as a key factor determining reproductive output. Wang [59] directly tested the relationship between lysis timing and burst size by constructing a series of lambda-phages that differed only in their lysis times. He then measured burst size and fitness of each strain and found that there was a positive relationship between lysis time and burst size. Furthermore, the strain with an intermediate lysis time had the highest fitness, indicating the existence of an optimal lysis time. Costs of adaptation and

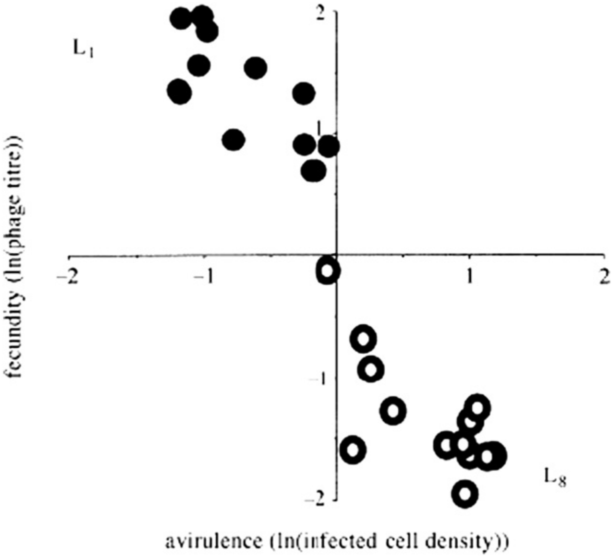

Fig. 1. The trade-off between phage avirulence and reproductive capacity measured as ln[infected cell density] and ln[phage titer], respectively. Closed and open symbols represent, respectively, values from L1 and L8 cultures (13 points each). A trade-off is indicated because the 13 L1 fecundities (all of which exceed the 13 L8 fecundities) are associated with 13 of the 14 lowest cell densities ($p < 10^{-5}$ for the model of random association of cell density with fecundity). Eleven of these L1 values are from selection I phage, one from selection II, and one from selection III (and similarly for L8 phage). Raw L1 and L8 values were standardized by subtracting the mean for all assay values obtained on the same day. Thus, if three L1 and three L8 values (with an observed average M) were obtained, each of the raw values was standardized by subtracting M, thereby removing the day-to-day heterogeneity in assay conditions that was found to be statistically significant. Note that ln[phage titer] values are concentrations of phage in cell supernatants and are not corrected for the density of cells producing those phages. The fact that cell densities were lower for L1 than for L8 means that the trade-off is even more extreme than shown here. From Ref. [46] with permission.