Population dynamics of bacteriophage T7 on heterogeneous *Escherichia coli* substrates

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How species invade new territories and how these range expansions influence the population's genotypes are important questions in the field of population genetics and have been mostly studied for expansions into homogeneous environments. To better understand range expansions in two-dimensional heterogeneous environments, we employ a system of bacteriophage T7 and two strains of *E. coli* that are susceptible and resistant to this phage. The bacteria form a heterogeneous lawn on which the bacteriophages expand, forming a plaque whose growth is followed over time. We study the expansion of the phage for different environments both experimentally and theoretically.

RANGE expansions, invasions of a species into a new habitat, are ubiquitous in nature and occur on very different time and length scales. Examples are the migration of humans out of Africa, species occupying areas previously covered by glaciers or devastated by fires, invasion of species into foreign habitats where they lack predators, the spread of diseases, and formation of microbe colonies. Though much has been understood about range expansions [1,2], many questions remain open or could not yet be addressed at all desired levels of understanding [3,4]. One of these open problems is the effect of spatial heterogeneities on range expansions itself and in consequence on the expanding population's genetic diversity.

To address the effects of heterogeneities we choose a combined experimental and theoretical approach, which has been proven successful in the past to study the expansion of microbial species on a homogeneous agar plate [5]. In our model system however, the expanding species is bacteriophage T7 which spreads on a two-dimensional lawn of *Escherichia coli*. The spatial expansion of this obligatory lytic bacteriophage manifests itself in the formation and growth of regions of dead bacteria (called plaques), which can be followed over time [6].

The heterogeneous environment in which the phage expands is made of patches of two different *E. coli* strains which differ in their interaction with the phage: one is susceptible to the phage and supports the phage population wave, the other is resistant and thus poses obstacles to the population front. Using a consumer inkjet printer [7] almost arbitrary environments can be created. Fluorescence microscopy allows observing the bacterial lawn consisting of the two differently labeled strains and the spread of the phage for simple and complex, regular and random environments.

To obtain a theoretical understanding we employ an existing reaction-diffusion model of plaque growth resembling the phage's life cycle [8], but generalized to heterogeneous environments. Within this model, the phage can diffuse while the bacterial lawn consisting of susceptible and resistant bacteria is assumed to not change over time (apart from cell lysis). Time-lapse images of plaque growth and numerical solutions of the reaction-diffusion model are compared quantitatively. In addition, we make use of simple geometric arguments to understand the front dynamics on a coarse-grained level and independent of the details of our model system. This is a first step to generalize our findings to other range expansions.

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