A bacterial mutualism exhibits strong oscillatory population dynamics

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***Short Abstract* — Because mutualistic interactions play a vital role in ecological communities, it is important to investigate how different ecological factors affect the dynamics and evolution of mutualistic relationships. Here, we use an experimental microbial system to study the dynamics of a cross-protection mutualism in which two bacterial strains cooperate to survive in a multidrug environment. Although one might expect such a mutualism to stabilize population dynamics, we observe strong oscillatory dynamics even when there is long-term coexistence between the two strains. We find that a simple model successfully explains our data and provides an intuitive way to think about mutualistic dynamics.**

***Keywords* — mutualism, evolutionary dynamics, antibiotic resistance, oscillations**

I. INTRODUCTION

Two species are called mutualistic if each of the species increases the fitness of its partner. Since mutualistic interactions between species are thought to be fundamental to the establishment and maintenance of ecological communities [1, 2], much research has focused on studying mutualisms in their natural setting. The view that emerged from such studies is that the nature of the interaction between species is context dependent: while two species can be mutualistic in a harsh environment, they can nonetheless become direct competitors in a more benign environment [3]. Since the complexity of the natural environment makes it challenging to disentangle how different factors affect the mutualism, laboratory experiments (e.g., [4]) can provide insight into the population and evolutionary dynamics that govern mutualistic relationships.

II. APPROACH

The bacterial mutualism in our model system arises from cross-protection against antibiotics. Two *E. coli* strains are each resistant to one of two antibiotics present in the environment: one strain inactivates ampicillin and the other inactivates chloramphenicol. By inactivating the antibiotic, resistant cells can protect other cells in the population that would otherwise be sensitive to the drug [5]. In the presence of both antibiotics, an obligatory mutualism arises because populations of different strains rely on each other to inactivate both antibiotics in the environment. To probe the dynamics of the mutualism, we experimentally track the populations of the two strains in a multidrug environment over multiple growth cycles.

III. RESULTS

As antibiotic concentrations increase, the two strains become increasingly dependent on each other for survival, with their interaction changing from being mostly competitive to being mostly mutualistic. Notably, the strains are able to grow in antibiotic concentrations that inhibit growth of either one of the strains alone, suggesting that the strains can form an obligatory mutualism. At still higher antibiotic concentrations, the two strains can no longer protect each other from the antibiotics and the entire bacterial population collapses.

Because the size of the total bacterial population varies little across many of the conditions where the population survives, one might expect to observe corresponding stability in the dynamics of the two subpopulations. However, we find that subpopulations are characterized by large oscillations.

We can explain the observed dynamics using a simple model that decomposes the observed dynamics into movements in "evolutionary space" (relative abundance of the two subpopulations) and in "population space" (abundance of the entire bacterial population).

Our results provide insight into the evolution of antibiotic resistance and, more generally, the evolutionary origin of cooperation, phenotypic diversity, and ecological stability.

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