

1 **Engineered cooperation and community dynamics**

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3 **Abstract**

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6 **Contents**

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12 **1 Introduction**

13 The major evolutionary transitions were not just the culmination of the Darwinian forces of
14 mutation and selection. Cooperation plays a major role in binding together a level of selection
15 so that it is possible for the ensemble of entities at one of the levels to be the target of selection
16 on the higher level (Maynard Smith and Szathmáry, 1995). Genes to cells, cells to organisms
17 and organisms to communities are some of the levels of selection where such a dynamic is
18 observed. It appears that when some form of conflict mediation is present resolving the issue
19 of what is good for the group as opposed to that of the individual, selection can focus on the

Table 1. Strains used in this study. FBR denotes feedback resistant - mutations that reduce limited gene regulation in response to cellular availability of amino acids

| Strain | Provides | Requires | Origin |
|-----------|------------|------------|--------|
| ADE4-FBR | Adenine | Lysine | Shou |
| LYS21-FBR | Lysine | Adenine | Shou |
| LEU4-FBR | Leucine | Tryptophan | Murray |
| TRP2-FBR | Tryptophan | Leucine | Murray |

next level of organisation. While numerous systems from RNA networks to human societies show cooperative behaviour, the trait needs explanation. On first glance it seems to violate the survival of the fittest argument. The conundrum can be explained via a number of compensatory mechanisms, ranging from the conceptual (Nowak, 2006a) to mechanistic arguments in mutualisms (Akçay E, 2015). In societies, cooperation is often enforced via an external entity that controls the levels of punishment or reward. Such delegation of management to a third party can emerge through rudimentary rules on behaviour (Sigmund et al., 2010). In bacterial communities though, synthetic cooperation can be induced via genetic manipulation (Shou et al., 2015; Campbell et al., 2015). In nutritionally depleted environments such as recently exposed volcanic material, communities of microbes are the pioneers facilitating the further growth of life (Kelly et al., 2014; Fujimura et al., 2016). The fact that such pioneers are often *communities* rather than *individual* species, critical in mediating biogeochemical cycles, bring forth the importance of cooperation right at the beginning of how life spread.

Why we need a simplified system Ecological networks are complex. Disentangling and understanding this complexity can be done at an abstract level employing information theory or network analysis. While this provides us with general properties of the interactions it is often impossible to pin down the principles which form the building blocks. One approach is to start with a simpler system with defined nature and number of interactions. Synthetically engineered communities are one way of achieving this (Momeni et al., 2013) **Why yeast?**

2 Materials and Methods

The strains we use come from the Murray lab M and Shou lab S. The $M = G_{\rightarrow L}^{\leftarrow W}, B_{\rightarrow W}^{\leftarrow L}$ community consists of two strains which are interdependent on the overproduction of tryptophan and leucine while $S = R_{\rightarrow K}^{\leftarrow A}, Y_{\rightarrow A}^{\leftarrow K}$ community is interdependent on adenine and lysine.

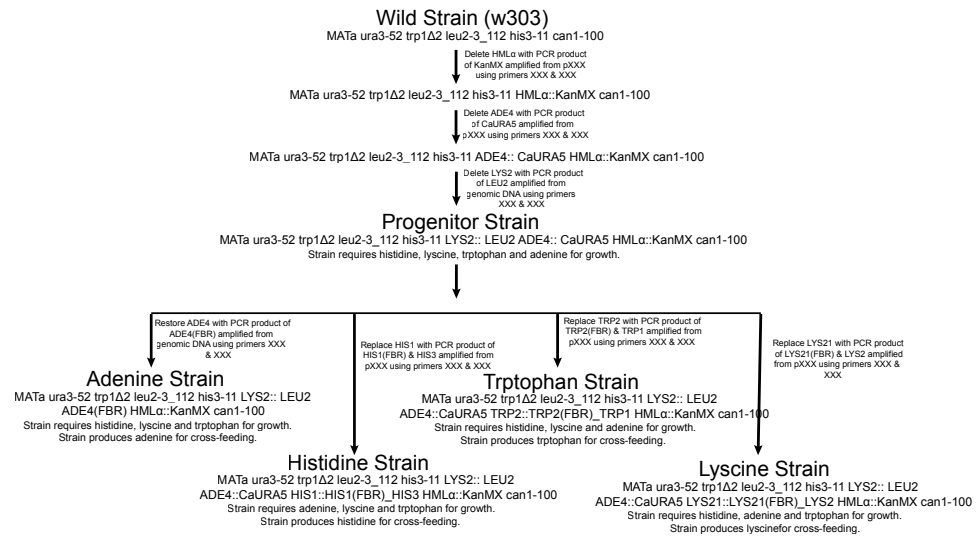


Figure 1. Outline

Growth curves

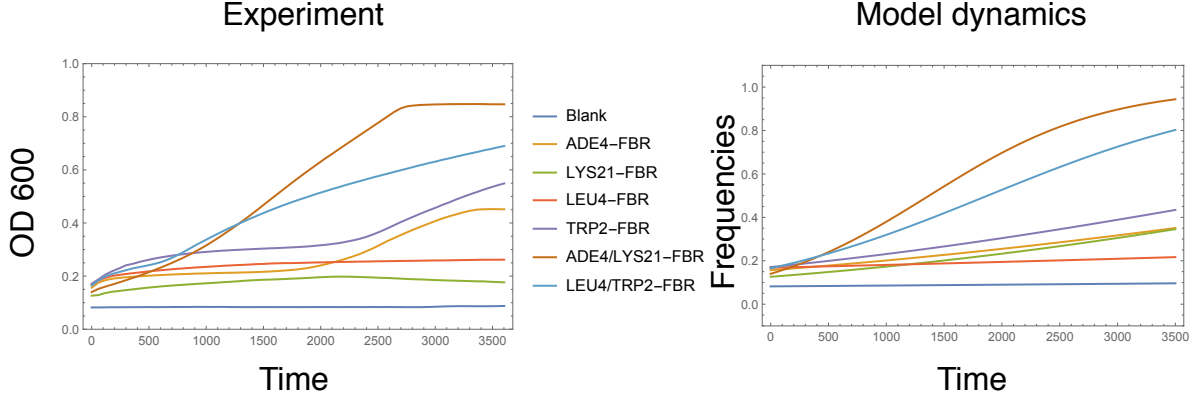


Figure 2. Growth rates

2.1 Individual growth rates

Following (Lenski et al., 1991) we measure the Malthusian growth parameters of each individual strain. We calculate the dynamics of individual yeast strains as they grow, independently with each having a carrying capacity of K . Thus the general dynamics can be represented can be captured by the standard logistic equations given by

$$\dot{x}_i = s_i x_i (1 - x_i / K) \quad (1)$$

and for two types grown together this is denoted by

$$\begin{aligned} \dot{x}_{ia} &= (r_{ia \rightarrow ia} x_{ia} + r_{ib \rightarrow ia} x_{ib}) (1 - (x_{ia} + x_{ib}) / K) \\ \dot{x}_{ib} &= (r_{ia \rightarrow ib} x_{ia} + r_{ib \rightarrow ib} x_{ib}) (1 - (x_{ia} + x_{ib}) / K) \end{aligned} \quad (2)$$

and we denote the frequency of this community by $x_i = x_{ia} + x_{ib}$. Comparing the model together with the data we see that the model dynamics captures well the population dynamics of the single inoculums as well as the community expansion.

While this simple model is able to capture the essential dynamics it can be further reduced to reflect the minimal required parameters to reproduce the interactions.

For a general hypercycle we can have the intrinsic growth rates of s_i for each of the individual species i and k_i as the feedback from the previous species in the cycle x_{i-1} . We can model this dynamic as a version of the replicator mutator equation, which is a limiting case of a number of different ecological models e.g. with a normalised carrying capacity.

We modeled the population dynamics of each community as a replicator-mutator system. The frequencies of the different strains are given by x_i and their Malthusian growth rates are f_i . The standard replicator-mutator equation is then denoted by (Nowak, 1992, 2006b):

$$\dot{x}_i = \sum_{j=0}^n r_{j \rightarrow i} x_j f_j - x_i \phi. \quad (3)$$

In this setup ϕ is defined so that the total population size of the two reactants remains constant. The fitness of type i in this case is assumed to be a frequency dependent quantity denoted by $f_i = 1$. Collating all these growth rates in a matrix \mathbf{Q}_{ij}

$$\mathbf{Q}_{i,j} = \begin{pmatrix} r_{1 \rightarrow 1} & r_{2 \rightarrow 1} & \cdots & r_{n \rightarrow 1} \\ r_{1 \rightarrow 2} & r_{2 \rightarrow 2} & \cdots & r_{n \rightarrow 2} \\ \vdots & \vdots & \ddots & \vdots \\ r_{1 \rightarrow n} & r_{2 \rightarrow n} & \cdots & r_{n \rightarrow n} \end{pmatrix} \quad (4)$$

55 The average fitness of the population is given by $\phi = \sum_{j=0}^n x_j f_j$
For a single inoculum of the strains, the equations reduce to

$$\dot{x}_i = s_i x_i - x_i \quad (5)$$

56 2.2 Two reactant system

For a simple system with just two types we can define the dynamics by,

$$\begin{aligned} \dot{x}_1 &= x_1(s_1 x_1 + k_1 x_2 - \phi) \\ \dot{x}_2 &= x_2(k_2 x_1 + s_2 x_2 - \phi). \end{aligned} \quad (6)$$

57 We denote s_i as the self-replication rate of type i and k_i as the rate at which the reactant is
58 generated by the reactant $i - 1$.

- 59 • Get basic growth rates of individual strains in complete media
- 60 • co-cultures in complete media
- 61 • co-cultures in reduced media
- 62 • competition experiment between communities (compete for space/other resources)
- 63 • modulate environment to see where they break down
- 64 • big exp

3 Results and Discussion

- Evolving mutualism for industry - microbes are often found in a consortia rather than individual species therefore also for the processes such as wastewater treatment, biofuel generation, oil spill cleanups etc., it might be possible to use symbiotic communities of bacteria rather than individual species (Zuroff and Curtis, 2012).
- Hypercycles were first describe as a model of pre-biotic evolution. Cooperation on the other hand can be assumed to be instrumental also from pre-biotic to contemporary timescales. When life colonises novel environments, it is hard to find it in isolation. Communities of bacteria are usually the pioneers in harsh environments from hydrothermal vents, lava flows and deep buried lava tubes. A few members of the consortia survive feeding of the inorganic matter but most of the community survives by a cross-feeding network.

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