



Competition and coexistence between a syntrophic consortium and a metabolic generalist, and its effect on productivity



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HIGHLIGHTS

- We predict which trade-offs will favor syntrophy.
- We show why competition may not optimize metabolite production.
- We apply the concept of relative nonlinearity to study positive interactions.
- We find a generalization of the R^* -rule for competition for multiple resources.

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ABSTRACT

Syntrophic interactions, where species consume metabolites excreted by others, are common in microbial communities, and have uses in synthetic biology. Syntrophy is likely to arise when trade-offs favor an organism that specializes on particular metabolites, rather than all possible metabolites. Several trade-offs have been suggested; however, few models consider different trade-offs to test which are most consistent with observed patterns. Here, we develop a differential equation model to study competition between a syntrophic processing chain, where each microbe can perform one step in metabolizing an initial resource to a final state, and a metabolic generalist that can perform all metabolic functions. We also examine how competition affects the production of the final metabolic compound. We find that competitive outcomes can be predicted by a generalization of the R^* -rule and relative nonlinearity. Therefore, the species that can persist at the lowest resource level is the competitive dominant in a constant environment, and species can coexist by partitioning variation in resources. We derive a simple rule for predicting production rates of the final metabolite, and show that competition may not maximize final metabolite production. We show that processing chains are inherently less efficient, because resources are lost during each step of the process. Our results also suggest which trade-offs are capable of explaining certain empirical observations. For example, processing chains appear to be more common in nutrient-rich environments; our model suggests that a specificity trade-off and an affinity-yield trade-off would not predict this, but a yield-maximum growth trade-off might.

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1. Introduction

Syntrophy, where one species consumes metabolites excreted by another, is a ubiquitous interaction in microbial communities (Wintermute and Silver, 2010; Zelezniak et al., 2015). One possible motif, here called a processing chain, is where multiple microbes can each perform one step in metabolizing an initial resource to a final product (Fig. 1). For example, different bacterial types convert ammonia to nitrite and nitrite to nitrate (Costa et al., 2006), or syringate to gallate and gallate to acetate (Kreikenbohm and Pfennig, 1985). Similarly, in wastewater treatment digesters,

organic waste is converted to methane over several steps, and each intermediate is metabolized by a different group of microbes (Batstone and Keller, 2002). However, it is by no means a metabolic or thermodynamic requirement that each organism perform only one step in these reactions. For example, recently discovered *Nitrospira* species can convert ammonia completely to nitrate (Daims et al., 2015; van Kessel et al., 2015), and *Holophaga foetida* can convert syringate completely to acetate (Bak et al., 1992). Many trade-offs have been proposed to explain why syntrophy might be favored, such as a specificity trade-off or an affinity-yield trade-off (Johnson et al., 2012; Litchman et al., 2015). However,

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while several models have explored the dynamics of processing chains (e.g., Bratbak and Thingstad, 1985; Dimitrova and Krastanov, 2014; El Hajji et al., 2010; Elkhader, 1991; Estrela et al., 2012; Powell, 1986), few have attempted to understand when a generalist could outcompete a processing chain; those that have each focused on a particular trade-off (e.g., Doebeli, 2002; Herron and Doebeli, 2013; Yomo et al., 1996), rather than developing a general model that can be adapted to different trade-offs. Such a model will help us to gain a basic understanding of microbial ecology by showing which trade-offs will favor or disfavor syntrophy under different conditions. In this paper, we develop a theoretical model to examine when competition will favor syntrophy, and when it will favor multi-step generalists.

A few empirical patterns are starting to emerge as to where syntrophic consortia are found. First, metabolic processes are more likely to be performed by a generalist when later steps are thermodynamically favorable (i.e., have a very negative Gibbs free energy), and more likely to be performed by a processing chain when the later steps are thermodynamically harder (Costa et al., 2006; González-Cabaleiro et al., 2015). Second, nutrient-rich environments appear more likely to have syntrophic consortia, whereas nutrient-poor environments appear more likely to have metabolic generalists (Costa et al., 2006). Finally, in laboratory cultures, *Escherichia coli* will often evolve into a syntrophic pair – from a generalist that converts sugar to CO_2 to a strain that converts sugar to acetate, and another that converts acetate to CO_2 – and this transformation is more likely in a chemostat than in serial batch cultures (Helling et al., 1987; Rozen and Lenski, 2000; Turner et al., 1996).

One explanation for syntrophy is that there is a *specificity trade-off*, such that increasing affinity for one resource lowers affinity for another (Gudelj et al., 2010; Litchman et al., 2015). A few models have generated predictions based on this trade-off (Doebeli, 2002; Yomo et al., 1996). These models suggest that syntrophy will evolve if rapidly taking up a single compound is favored over slowly taking up many compounds (Doebeli, 2002). However, such models cannot explain why syntrophy should be favored in nutrient-rich environments. Additionally, models developed to analyze this trade-off have assumed that intermediate compounds are extremely leaky (Doebeli, 2002; Yomo et al., 1996). For example, Doebeli (2002) assumed that a generalist *E. coli* would convert sugar to acetate, excrete the acetate into the environment, reabsorb it, and then convert it to CO_2 . However, some multi-step generalists have been shown to lack the transport proteins needed to excrete intermediate compounds (Daims et al., 2015), as is predicted by optimization models (Pfeiffer and Bonhoeffer, 2004). It is not clear how predictions would change if generalists could avoid excreting intermediate compounds, though models of public goods suggest that multi-step generalists would be favored by

even a tiny reduction in leakage (Gore et al., 2009).

An alternative explanation is that there is a *yield-maximum growth trade-off*, such that single-step specialists have higher maximum growth rates, but multi-step generalists can produce more biomass per unit resource (Costa et al., 2006; Pfeiffer and Bonhoeffer, 2004). A mechanistic model showed that this trade-off would arise if (a) microbes pay a cost for each metabolic step, and (b) growth is a saturating function of ATP gained from each metabolic step (Pfeiffer and Bonhoeffer, 2004). Unfortunately, due to the complexities of this model, this trade-off has not previously been analyzed in a variable environment. Thus, it is unclear whether its predictions would differ between a (constant) chemostat-type model and a (variable) serial batch culture-type model.

Additionally, the *affinity-yield trade-off* suggests that species who can rapidly take up a resource generate less biomass per unit resource (MacLean and Gudelj, 2006). We know of no models that have analyzed this trade-off to determine how it will affect coexistence between a processing chain and a generalist.

In addition to improving our understanding of microbial ecology, an understanding of syntrophy has applications to synthetic biology (Escalante et al., 2015; Mee and Wang, 2012). Syntrophic consortia can be used to accumulate biomass (Harvey et al., 2014), produce useful compounds (Batstone and Keller, 2002; Sabra et al., 2010), and degrade unwanted material (Katsuyama et al., 2009). However, syntrophy may not always be favored by competition. Because bacteria have short generation times, high mutation rates, and the ability to transfer genes horizontally, mutants with altered metabolic capacity may commonly arise. When they do, selection will favor the organism that maximizes fitness, rather than the design goals. However, in some cases, we expect that fitness and design goals may be intertwined. In this paper, we choose a particular design goal – maximum end-product production, a goal of anaerobic digesters (Batstone and Keller, 2002; Dimitrova and Krastanov, 2014; Weedermann et al., 2013) – and determine whether competition will select for an optimal consortia from a design standpoint.

In this paper, we study competition in a system of syntrophic microbes. We examine when the members of an n -species processing chain can outcompete or coexist with a generalist that can fully metabolize each resource (Fig. 1). We then determine how much final compound is produced in each possible community. We answer the following interrelated questions:

- (1) What is the outcome of competition between a processing chain and a metabolic generalist?
- (2) How does the production of the final compound depend on each parameter in the model?
- (3) Will competition maximize production of the final compound?

We examine these questions both in a stable environment and when resource inputs vary. Our analysis is fairly general, and makes few assumptions about parameter values. However, we conclude by discussing how various proposed trade-offs are expected to affect competitive outcomes.

2. The model

We model competition between a syntrophic processing chain of microbes (named species 1, 2, ..., n), and a generalist who can consume all relevant compounds. Fig. 1 shows a graphical representation of the model, Table 1 lists the relevant parameters, and Table 2 lists the variables used. Our equations are based on the Monod model, a standard model for chemostat dynamics (Monod, 1949). Here, fresh medium is supplied and old medium is withdrawn at rate d , and with it, any microbes or resources. The initial

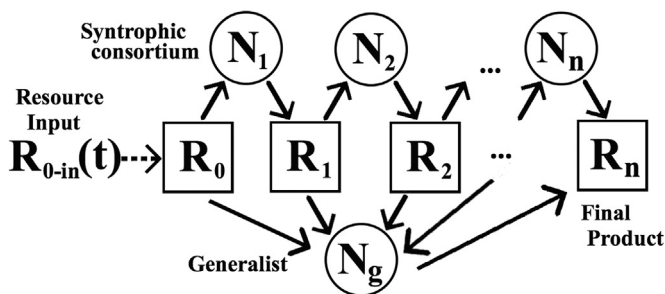


Fig. 1. Schematic diagram of competition between an n -member syntrophic processing chain (N_1 through N_n) and a single generalist species (N_g). Each syntrophic species consumes one resource (R_j), and metabolizes it one step (i.e., from R_j to R_{j+1}). The generalist can consume every resource, and metabolizes each of them to the final compound (R_n).

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