20251029 - 20251102 Summary

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1 General System in Starvation Limit

1.1 Example Calculation for Four Partitions

The solution for four-sector partition is

$$Y_1 = \frac{1}{2}\left[\sqrt{\left(\frac{a_1\theta_2}{b\theta_1} + k_1 - 1\right)^2 + 4k_1} - \left(\frac{a_1\theta_2}{b\theta_1} + k_1 - 1\right)\right], \tag{1a}$$

$$Y_2 = \frac{1}{2}\left\{\sqrt{\left[\frac{a_2\theta_3}{b\theta_1} + k_2 - (1 - Y_1)\right]^2 + 4k_2(1 - Y_1)} - \left[\frac{a_2\theta_3}{b\theta_1} + k_2 - (1 - Y_1)\right]\right\}, \tag{1b}$$

$$Y_3 = \frac{1}{2}\left\{\sqrt{\left[\frac{a_3\theta_4}{b\theta_1} + k_3 - (1 - Y_1 - Y_2)\right]^2 + 4k_3(1 - Y_1 - Y_2)} - \left[\frac{a_3\theta_4}{b\theta_1} + k_3 - (1 - Y_1 - Y_2)\right]\right\}, \tag{1c}$$

$$Y_4 = \left(\frac{a_3\theta_4}{b}\right)\frac{Y_3}{k_3 + Y_3}, \quad Y_5 = \frac{\theta_2}{\theta_1}Y_4, \quad Y_6 = \frac{\theta_3}{\theta_1}Y_4, \quad Y_7 = \frac{\theta_4}{\theta_1}Y_4. \tag{1d}$$

Expand in the limit of small b, then the growth rate $\lambda = bY^*$ is given by

$$\lambda = b\theta_1\left[1 - b\theta_1\left(\frac{k_1}{a_1\theta_2} + \frac{k_2}{a_2\theta_3} + \frac{k_3}{a_3\theta_4}\right)\right] + O(b^3), \tag{2}$$

similar to that of the three-sector case. Let $A_4 = \sqrt{\frac{k_1}{a_1}} + \sqrt{\frac{k_2}{a_2}} + \sqrt{\frac{k_3}{a_3}}$. Carrying out the same computations of Lagrange multipliers, we find

$$\theta_2 : \theta_3 : \theta_4 = \sqrt{\frac{k_1}{a_1}} : \sqrt{\frac{k_2}{a_2}} : \sqrt{\frac{k_3}{a_3}} \tag{3}$$

and

$$\frac{\theta_1}{\theta_{j+1}} = \sqrt{\frac{a_j}{k_j}}\left(\frac{1}{\sqrt{b}} - A_4 + \frac{1}{2}A_4^2\sqrt{b}\right) + O(b), \quad j = 1, 2, 3. \tag{4a}$$

$$\tag{4b}$$

Solve for θ_1 by the normalization condition, then solve for $\theta_{j=2,3,4}$. This gives similar formulae as in the three-sector case but with A replaced by A_4.

$$\theta_1 = \left(1 + \frac{\theta_2}{\theta_1} + \frac{\theta_3}{\theta_1} + \frac{\theta_4}{\theta_1}\right)^{-1} = 1 - A_4\sqrt{b} + \frac{1}{2}A_4^3 b^{3/2} + O(b^{5/2}), \tag{5a}$$

$$\theta_{j+1} = \sqrt{\frac{k_j}{a_j}}\left[\sqrt{b} - \frac{1}{2}A_4^2 b^{3/2} +\right] + O(b^{5/2}), \quad j = 1, 2, 3. \tag{5b}$$

We have an expression that is invariant under permutation of indices $1 \leftrightarrow 2 \leftrightarrow 3$.

$$\boxed{\lambda = b - 2A_4 b^{3/2} + \left(\frac{5}{2}A_4^2 + \frac{1}{2}B_4 - F_4\right) b^2 + O(b^{5/2}),} \tag{6}$$

where

$$B_4 = \frac{k_1}{a_1} + \frac{k_2}{a_2} + \frac{k_3}{a_3}, \quad F_4 = \frac{1}{a_1} + \frac{1}{a_2} + \frac{1}{a_3}. \tag{7}$$

1.2 Proof of Proposition

As suggested by the above calculation, we claim that in the general n-sector partition model during starvation (small b), the partition strengths are given by

$$\theta_1 = 1 - A\sqrt{b} + \frac{1}{2}A^3 b^{3/2} + O(b^{5/2}), \tag{8a}$$

$$\theta_j = \sqrt{\frac{k_{j-1}}{a_{j-1}}}\left[\sqrt{b} - \frac{1}{2}A^2 b^{3/2} + O(b^{5/2})\right], \quad (2 \le j \le n), \tag{8b}$$

where

$$A = \sqrt{\frac{k_1}{a_1}} + \sqrt{\frac{k_2}{a_2}} + \cdots + \sqrt{\frac{k_n}{a_n}}. \tag{9}$$

Showing this is equivalent to showing that in a system of n partitions, the following property holds:

Proposition 1.1. *In the $b \to 0$ limit, the biomass fraction Y_n of an n-partition system has the form*

$$Y_n = \theta_1 - b\theta_1^2 \left(\sum_{i=1}^{n-1} \frac{k_i}{a_i \theta_{i+1}} \right) + O(b^2). \tag{10}$$

Proof. First consider the following expansion

$$\frac{1}{2}\left[\sqrt{(z+u)^2 + 4k} - (z+u)\right] = \frac{k}{z} - \frac{ku}{z^2} + O(z^{-3}), \tag{11}$$

when z is very large. In the $b \to 0$ limit, notice that the quantity $\alpha_i = \frac{a_i \theta_{i+1}}{b\theta_1} \to \infty$.

The n-sector system consists of both terminal nodes and nonterminal nodes, whose biomass fraction expression have distinct forms.

(1) Nonterminal nodes: These are the nodes with index $1 \le i \le n-1$. Apply the above expansion and notice that $\alpha_i \to \infty$.

$$Y_1 = \frac{1}{2}\left[\sqrt{(\alpha_1 + k_1 - 1)^2 + 4k_1} - (\alpha_1 + k_1 - 1)\right] = \frac{k_1}{\alpha_1} + O(b^2) = \frac{bk_1\theta_1}{a_1\theta_2} + O(b^2), \tag{12}$$

$$\begin{aligned} Y_i &= \frac{1}{2}\left[\sqrt{\left(\alpha_i + k_i - \left(1 - \sum_{r=1}^{i-1} Y_r\right)\right)^2 + 4k_i} - \left(\alpha_i + k_i - \left(1 - \sum_{r=1}^{i-1} Y_r\right)\right)\right] \\ &= \frac{k_i}{\alpha_i} + O(b^2) = \frac{bk_i\theta_1}{a_i\theta_{i+1}} + O(b^2), \end{aligned} \tag{13}$$

for $2 \le i \le n-1$. We used the fact that $\sum_{r=1}^{i-1} Y_r = O(b)$ vanishes in the $b \to 0$ limit.

(2) Terminal nodes: These are the nodes with index $n \le i \le 2n-1$. The biomass fractions satisfy

$$Y_{n+1} = \frac{\theta_2}{\theta_1} Y_n, \quad Y_{n+2} = \frac{\theta_3}{\theta_1} Y_n, \quad \ldots, \quad Y_{2n-1} = \frac{\theta_n}{\theta_1} Y_n, \tag{14}$$

subject to the condition $\sum_{i=1}^{n} \theta_i = 1$. Using $\sum_{i=1}^{2n-1} Y_i = 1$, we have

$$Y_n + Y_{n+1} + \ldots + Y_{2n-1} = \left(1 + \frac{\theta_2}{\theta_1} + \ldots + \frac{\theta_n}{\theta_1}\right) Y_n = 1 - \sum_{i=1}^{n-1} Y_i, \tag{15}$$

and hence

$$Y_n = \frac{\theta_1}{\theta_1 + \cdots + \theta_n}\left(1 - \sum_{i=1}^{n-1} Y_i\right) = \theta_1 \left(1 - \sum_{i=1}^{n-1} Y_i\right). \tag{16}$$

Up to order $O(b)$, plug in previous results for Y_i, $1 \le i \le n-1$, we have

$$Y_n = \theta_1 - b\theta_1^2 \left(\frac{k_1}{a_1\theta_2} + \frac{k_2}{a_2\theta_3} + \cdots + \frac{k_{n-1}}{a_{n-1}\theta_n} \right) + O(b^2). \tag{17}$$

□

According to Proposition 1.1, the Lagrangian function for our system is given by

$$L(\theta, \mu) = b\theta_1 - b^2\theta_1^2 \left(\sum_{i=1}^{n-1} \frac{k_i}{a_i\theta_{i+1}} \right) - \mu \left(\sum_{i=1}^{n} \theta_i - 1 \right). \tag{18}$$

Then the relevant partial derivatives are

$$\frac{\partial L}{\partial \theta_1} = b - 2b^2\theta_1 \left(\sum_{i=1}^{n-1} \frac{k_i}{a_i\theta_{i+1}} \right) = \mu, \tag{19a}$$

$$\frac{\partial L}{\partial \theta_j} = b^2\theta_1^2 \left(\frac{k_{j-1}}{a_{j-1}\theta_j^2} \right) = \mu, \quad (2 \le j \le n). \tag{19b}$$

The $2 \le j \le n$ equations can be used to solve for the ratio, which agrees with our claim:

$$\theta_2 \,:\, \theta_3 \,:\, \cdots \,:\, \theta_n = \sqrt{\frac{k_1}{a_1}} \,:\, \sqrt{\frac{k_2}{a_2}} \,:\, \cdots \,:\, \sqrt{\frac{k_{n-1}}{a_{n-1}}}. \tag{20}$$

Moreover, substituting back into the normalization condition and expanding in powers of b gives the expressions for θ_1 and $\theta_{j=2,\ldots,n}$ as claimed:

$$\theta_1 = 1 - A\sqrt{b} + \frac{1}{2}A^3 b^{3/2} + O(b^{5/2}), \tag{21a}$$

$$\theta_j = \sqrt{\frac{k_{j-1}}{a_{j-1}}} \left[\sqrt{b} - \frac{1}{2}A^2 b^{3/2} + O(b^{5/2}) \right], \quad (2 \le j \le n), \tag{21b}$$

$$A = \sqrt{\frac{k_1}{a_1}} + \sqrt{\frac{k_2}{a_2}} + \cdots + \sqrt{\frac{k_{n-1}}{a_{n-1}}}. \tag{21c}$$

Therefore, the $\sqrt{b}$ relationship is universal for all n-sector partition models during starvation, for all $n \ge 2$. Note that θ_1 and λ in this case are invariant under exchange of indices.

2 Two-Sector Proteome Partition Model

Consider a simplified model with only two sectors: the translational sector and the ribosomal sector. This will help us understand the basic principles of the more complex three-sector model. Many results from the two-sector model can be extended to the three-sector, and hence n-sector case.

In the (Y, N) coordinates, we can write:

$$\frac{\mathrm{d}Y_1}{\mathrm{d}t} = bY_2 - \frac{aY_1Y_3}{k+Y_1} - bY_2Y_1, \tag{22a}$$

$$\frac{\mathrm{d}Y_2}{\mathrm{d}t} = \theta_1\left(\frac{aY_1}{k+Y_1}\right)Y_3 - bY_2^2, \tag{22b}$$

$$\frac{\mathrm{d}Y_3}{\mathrm{d}t} = \theta_2\left(\frac{aY_1}{k+Y_1}\right)Y_3 - bY_2Y_3 \tag{22c}$$

The unique nonnegative steady states for this system are given by

$$\boxed{\begin{aligned}
Y_1 &= \frac{1}{2}\left[\sqrt{\left(\frac{a\theta_2}{b\theta_1}+k-1\right)^2+4k}-\left(\frac{a\theta_2}{b\theta_1}+k-1\right)\right], &(23a)\\
Y_2 &= \left(\frac{a\theta_2}{b}\right)\frac{Y_1}{k+Y_1} &(23b)\\
Y_3 &= \left(\frac{a\theta_2^2}{b\theta_1}\right)\frac{Y_1}{k+Y_1} &(23c)
\end{aligned}}$$

as in the general n-sector case which we will see later.

2.1 Starvation and Overabundance Limits

In the $b \to 0$ limit, apply Lagrangian multipliers on $L(\theta, \mu) = bY_2(\theta) - \mu(\theta_1 + \theta_2 - 1)$ gives

$$Y_1 = k\left(\frac{b\theta_1}{a_1\theta_2}\right) + k(1-k)\left(\frac{b\theta_1}{a_1\theta_2}\right)^2 + O(b^3), \tag{24a}$$

$$Y_2 = \theta_1\left[1 - k\left(\frac{b\theta_1}{a_1\theta_2}\right) + k(1-k)\left(\frac{b\theta_1}{a_1\theta_2}\right)^2\right] + O(b^3), \tag{24b}$$

$$Y_3 = \theta_2\left[1 - k\left(\frac{b\theta_1}{a_1\theta_2}\right) + k(1-k)\left(\frac{b\theta_1}{a_1\theta_2}\right)^2\right] + O(b^3). \tag{24c}$$

and

$$\frac{\partial L}{\partial \theta_1} = b - 2b^2\theta_1 \left(\frac{k_1}{a_1\theta_2} + \frac{k_2}{a_2\theta_3}\right) - \mu = 0, \tag{25a}$$

$$\frac{\partial L}{\partial \theta_3} = \left(\frac{k_2\theta_1^2}{a_2\theta_3^2}\right) b^2 - \mu = 0, \tag{25b}$$

and hence

$$\theta_1 = 1 - \sqrt{\frac{k}{a}}\sqrt{b} + \frac{1}{2}\left(\frac{k}{a}\right)^{3/2} b^{3/2} + O(b^{5/2}), \tag{26a}$$

$$\theta_2 = \sqrt{\frac{k}{a}}\sqrt{b} - \frac{1}{2}\left(\frac{k}{a}\right) b^{3/2} + O(b^{5/2}), \tag{26b}$$

$$\lambda = b - 2\sqrt{\frac{k}{a}} b^{3/2} - \left(\frac{1-2k}{a}\right) b^2 + O(b^{5/2}). \tag{26c}$$

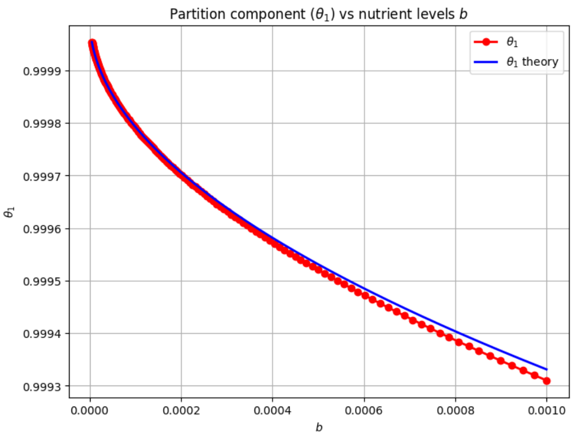

Figure 1: θ_1 in the starvation limit.

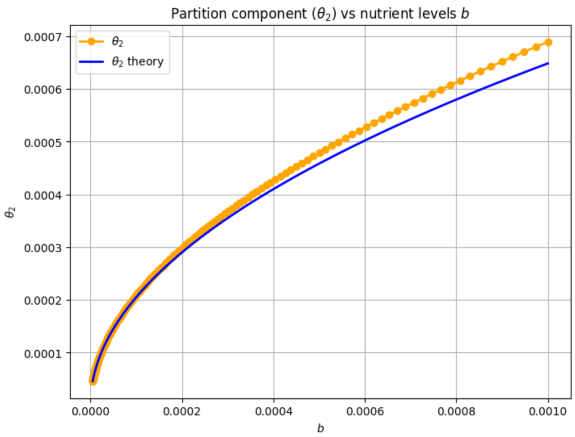

Figure 2: θ_2 in the starvation limit.

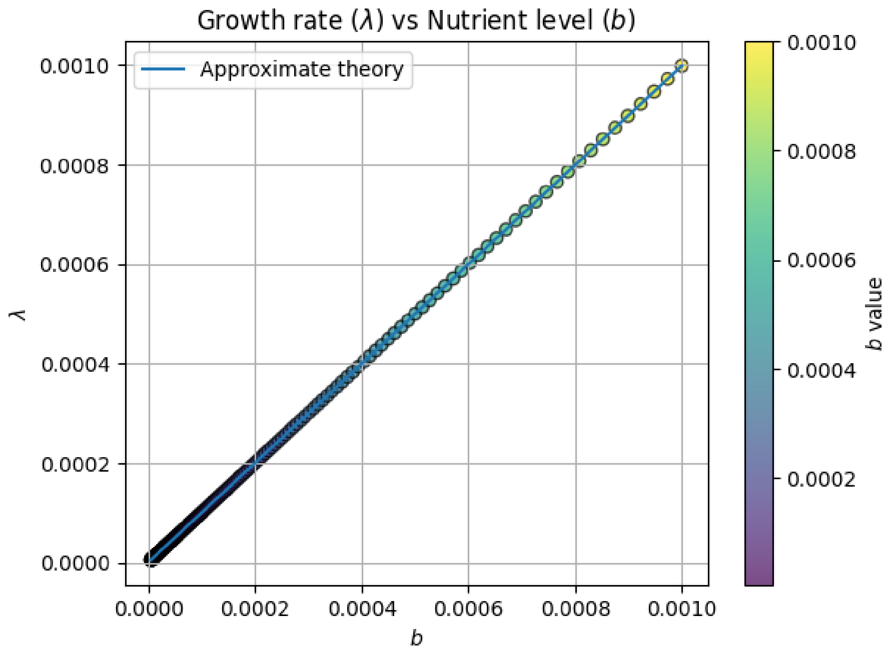

Figure 3: Growth rate λ versus b in the starvation limit.

On the other hand, in the $b \to \infty$ limit we have

$$Y_1 = 1 - \frac{1}{1+k}\left(\frac{a\theta_2}{b\theta_1}\right) + \frac{k}{(1+k)^3}\left(\frac{a\theta_2}{b\theta_1}\right)^2 + O\left(b^{-3}\right), \tag{27a}$$

$$Y_2 = \theta_1\left[\frac{1}{1+k}\left(\frac{a\theta_2}{b\theta_1}\right) - \frac{k}{(1+k)^3}\left(\frac{a\theta_2}{b\theta_1}\right)^2\right] + O\left(b^{-3}\right), \tag{27b}$$

$$Y_3 = \theta_2\left[\frac{1}{1+k}\left(\frac{a\theta_2}{b\theta_1}\right) - \frac{k}{(1+k)^3}\left(\frac{a\theta_2}{b\theta_1}\right)^2\right] + O\left(b^{-3}\right). \tag{27c}$$

Then apply Lagrangian multipliers on L up to order b^{-2}, where

$$L(\theta, \mu) = b\theta_1\left[\frac{1}{1+k}\left(\frac{a\theta_2}{b\theta_1}\right) - \frac{k}{(1+k)^3}\left(\frac{a\theta_2}{b\theta_1}\right)^2\right] - \mu(\theta_1 + \theta_2 - 1). \tag{28}$$

Then we have

$$\frac{\partial L}{\partial \theta_1} = \frac{ka^2}{(1+k)^3}\left(\frac{\theta_2}{\theta_1}\right)^2 \frac{1}{b} - \mu = 0, \tag{29a}$$

$$\frac{\partial L}{\partial \theta_2} = \frac{a}{1+k} - \frac{k}{(1+k)^3}\frac{2a_1^2\theta_2}{b\theta_1} - \mu = 0. \tag{29b}$$

Solving for θ_2/θ_1 gives

$$\frac{a}{1+k} - \frac{2ka^2}{(1+k)^3}\left(\frac{\theta_2}{\theta_1}\right)\frac{1}{b} = \mu = \frac{ka^2}{(1+k)^2}\left(\frac{\theta_2}{\theta_1}\right)^2\frac{1}{b} \tag{30}$$

$$\implies \frac{\theta_2}{\theta_1} = -1 + \sqrt{1 + \frac{(1+k)^2}{ka}b}, \qquad \text{up to order } O(b). \tag{31}$$

We have $\underline{\theta_1 = O(1/\sqrt{b}),\ \theta_2 = O(1)}$. Unlike the $b \to 0$ limit, the $b \to \infty$ limit is different from the $n \geq 3$-sector models in that we can solve for θ_2/θ_1 nicely without further approximations. More precisely, we have

$$\boxed{\begin{aligned}
\theta_1 &= \frac{\sqrt{k}}{1+k}\sqrt{\frac{a}{b}} - \frac{k}{2(1+k)^2}\left(\frac{a}{b}\right)^{3/2} + O\left((a/b)^{5/2}\right), && \text{(32a)}\\
\theta_2 &= 1 - \frac{\sqrt{k}}{1+k}\sqrt{\frac{a}{b}} + \frac{k}{2(1+k)^2}\left(\frac{a}{b}\right)^{3/2} + O\left((a/b)^{5/2}\right), && \text{(32b)}\\
\lambda &= \frac{a}{1+k} - \frac{2a\sqrt{k}}{(1+k)^2}\sqrt{\frac{a}{b}} + \frac{2k}{(1+k)^3}\frac{a^2}{b} + O\left(b^{-2}\right). && \text{(32c)}
\end{aligned}}$$

2.2 Bottleneck Limit

In the $a \to 0$ limit, the expansion is identical to the $b \to \infty$ limit for the two-sector model, since <u>it is only meaninful to consider the dimensionless parameter a/b in the system</u>, instead of a and b as absolute quantities. Applying Lagrange multipliers on L gives, as before,

$$w\,\frac{\theta_2}{\theta_1} = -1 + \sqrt{1 + \frac{(1+k)^2}{ka}b}, \qquad \text{up to order } O(b). \tag{33}$$

We have $\underline{\theta_1 = O(\sqrt{a}),\ \theta_2 = O(1)}$, and θ_1, θ_2 are as given above.

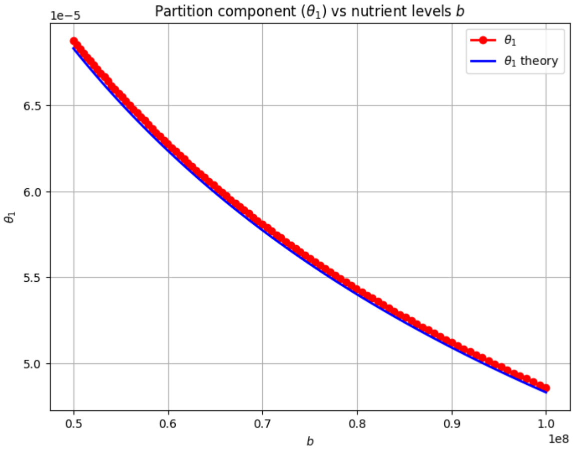

Figure 4: θ_1 in the overabundance limit.

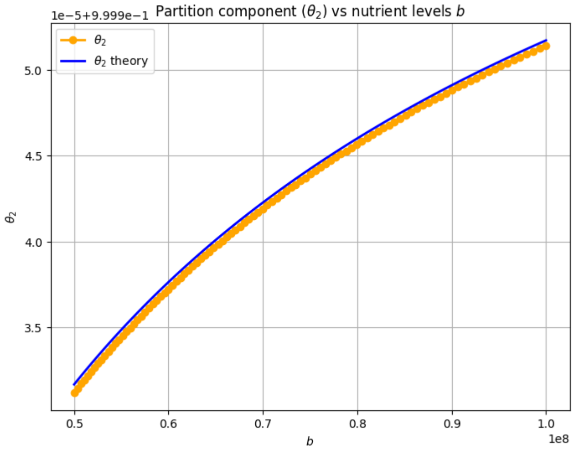

Figure 5: θ_2 in the overabundance limit.

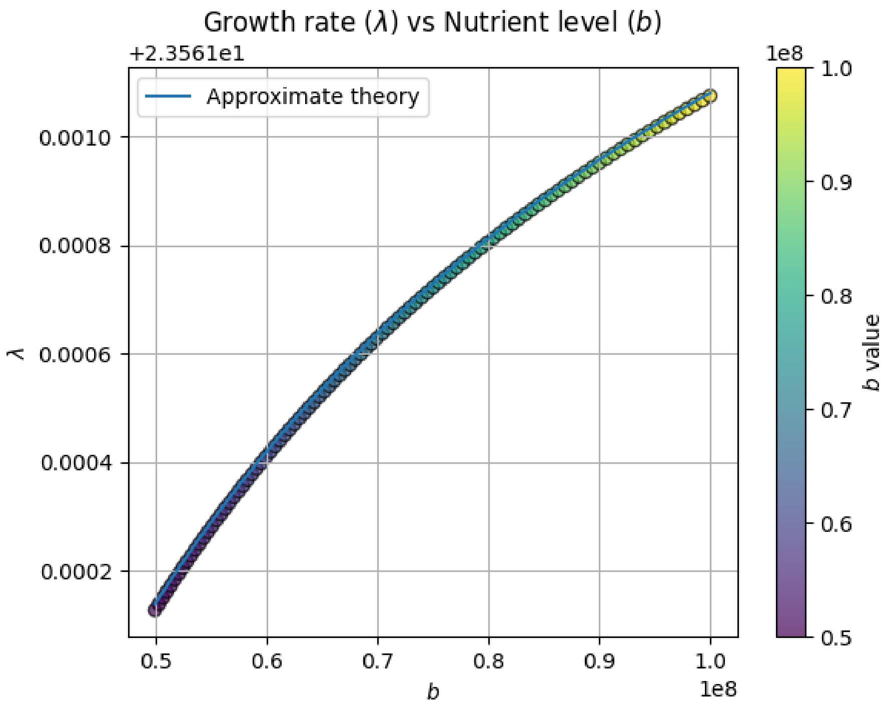

Figure 6: Growth rate λ versus b in the overabundance limit.

3 Special Functions for MM and MA Calculations

3.1 Michaelis-Menten Calculations

The equation

$$1 - mx = \frac{cx}{k + x} \tag{34}$$

is ubiquitous in the analysis of Michaelis-Menten fluxes. It admits the nonnegative solution given by

$$p_{\mathrm{MM}}(c, k, m) = \frac{1}{2m}\left[(1 - c - mk) + \sqrt{(1 - c - mk)^2 + 4mk}\right]. \tag{35}$$

The quantity $p_{\mathrm{MM}}(c, k, m)$ always lies between 0 and $1/m$, is an increasing function of c, m, and a decreasing function of k. For our system, we can express the fixed point solution as

$$\boxed{\begin{aligned} Y_1^* &= p_{\mathrm{MM}}\left(\frac{a_1\theta_2}{b\theta_1}, k_1, 1\right) \equiv p_{\mathrm{MM}}(c_1, k_1, m_1), && \text{(36a)} \\ Y_2^* &= p_{\mathrm{MM}}\left(\frac{a_2\theta_3}{a_1\theta_2}\frac{k_1 + Y_1^*}{Y_1^*}, k_2, \frac{b\theta_1}{a_1\theta_2}\frac{k_1 + Y_1^*}{Y_1^*}\right) \equiv p_{\mathrm{MM}}(c_2, k_2, m_2), && \text{(36b)} \\ Y_{k+2}^* &= \theta_k\left(1 - Y_1^* - Y_2^*\right), \quad k = 1, 2, 3. && \text{(36c)} \end{aligned}}$$

We can express the general solution to the n-partition model using the p_{MM} function. This will help us in showing the system has a unique nonnegative fixed point.

$$\boxed{\begin{aligned} Y_1^* &= p_{\mathrm{MM}}\left(\frac{a_1\theta_2}{b\theta_1}, k_1, 1\right), && \text{(37a)} \\ Y_i^* &= p_{\mathrm{MM}}\left(\frac{a_i\theta_{i+1}}{a_{i-1}\theta_i}\frac{k_{i-1} + Y_{i-1}^*}{Y_{i-1}^*}, k_i, \frac{b\theta_1}{a_{i-1}\theta_i}\frac{k_{i-1} + Y_{i-1}^*}{Y_{i-1}^*}\right), \quad i = 2, \ldots, n-1, && \text{(37b)} \\ Y_{k+n-1}^* &= \theta_k\left(1 - \sum_{i=1}^{k-1} Y_k^*\right), \quad k = 1, \ldots, n. && \text{(37c)} \end{aligned}}$$

Since $p_{\mathrm{MM}}(c, k, m)$ is the intersection of the line $1 - mx = 0$ and the Michaelis-Menten curve $(cx)/(k+x)$, it is clear that for any $c, k, m > 0$, there is a unique nonnegative solution to equation (34). By iterating p_{MM} and applying the Intermediate Value Theorem, we immediately see that the n-partition model has a unique nonnegative fixed point for any choice of positive parameters.

Let's consider the relevant limits of $p_{\mathrm{MM}}(c,k,m)$ for the $b \to 0$ and $b \to \infty$ limits. When $b \to 0$, we have $c_1 \to \infty$ and $c_2 \to \infty$. Here, even though it seems like $m_2 \to 0$, we simultaneously have $Y_1^* \to 0$, so in fact $m_2 = O(1)$. When $b \to \infty$, we have $c_1 \to 0$, $Y_1^* \to 1$, and hence $m_2 \to \infty$.

(1) $c \to 0$: By direct expansion of $p(c,k,m)$ about $c = 0$, we have

$$\boxed{p(c,k,m) = \frac{1}{m} - \frac{c}{m\,(km+1)} + \frac{k}{(km+1)^3}\,c^2 + \frac{k\,(1-km)}{(km+1)^5}\,c^3 + O(c^4).} \tag{38}$$

(2) $c \to \infty$: By direct expansion of $p(c,k,m)$ about $c = \infty$, we have

$$\boxed{p(c,k,m) = \frac{k}{c} + \frac{k - k^2 m}{c^2} + \frac{k\,(k^2m^2 - 3km + 1)}{c^3} + O(c^{-4}).} \tag{39}$$

(3) $m \to \infty$: By direct expansion of $p(c,k,m)$ about $m = \infty$, we have

$$\boxed{p(c,k,m) = \frac{1}{m} - \frac{c}{k\,m^2} + \frac{c(1+c)}{k^2\,m^3} + O(m^{-4}).} \tag{40}$$

3.1.1 Starvation Limit Calculations

We use the special function expansions to illustrate the leading-order behavior of the system in the starvation ($b \to 0$) and overabundance ($b \to \infty$) limits.

When $b \to 0$, we have $c_1 \to \infty$, $c_2 \to \infty$, and $m_2 = O(1)$. Therefore, using the $c \to \infty$ expansion on c_1, we have

$$\boxed{Y_1 = k_1 \left(\frac{b\theta_1}{a_1\theta_2}\right) + k_1(1-k_1)\left(\frac{b\theta_1}{a_1\theta_2}\right)^2 + O\left(n_1^3\right),} \tag{41}$$

and

$$\frac{Y_1^*}{k_1 + Y_1^*} = \left(\frac{b\theta_1}{a_1\theta_2}\right) - k_1\left(\frac{b\theta_1}{a_1\theta_2}\right)^2 + O\left(n_1^3\right), \tag{42}$$

$$\frac{k_1 + Y_1^*}{Y_1^*} = \left(\frac{a_1\theta_2}{b\theta_1}\right) + k_1 + O\left(n_1^3\right). \tag{43}$$

Then, using the same expansion on c_2, we have

$$\frac{1}{c_2} = \left(\frac{a_1\theta_2}{a_2\theta_3}\right)\left(\frac{Y_1^*}{k_1+Y_1^*}\right) = \frac{b\theta_1}{a_2\theta_3} - k_1\left(\frac{b\theta_1}{a_2\theta_3}\right)\left(\frac{b\theta_1}{a_1\theta_2}\right) + O\left(n_2^3\right), \tag{44}$$

$$m_2 = \frac{b\theta_1}{a_1\theta_2}\frac{k_1+Y_1^*}{Y_1^*} = 1 + k_1\left(\frac{b\theta_1}{a_1\theta_2}\right) + O\left(n_1^2\right). \tag{45}$$

Applying the $c \to \infty$ expansion on Y_2^*, we have

$$\boxed{Y_2 = k_2\left(\frac{b\theta_1}{a_2\theta_3}\right) - \frac{k_2(a_1k_2\theta_2 - a_1\theta_2 + a_2k_1\theta_3)}{a_1\theta_2}\left(\frac{b\theta_1}{a_2\theta_3}\right)^2 + O\left(n_2^3\right), \qquad (46)}$$

so Y_3^*, Y_4^*, Y_5^* can be computed accordingly. <u>This agrees with the full calculation.</u> In effect, we are computing the series expansion with respect to the dimensionless quantity $n_1 = b\theta_1/a_1\theta_2$ and $n_2 = b\theta_1/a_2\theta_3$. Similar analysis for the overabundance limit $b \to \infty$ using the $c \to 0$ expansion also agrees with the full calculation.

$$Y_1 = k_1\left(\frac{b\theta_1}{a_1\theta_2}\right) + \frac{k_1\theta_2(1-k_1)}{\theta_2}\left(\frac{b\theta_1}{a_1\theta_2}\right)^2 + O\left(n_1^3\right), \tag{47}$$

$$Y_2 = k_2\left(\frac{b\theta_1}{a_2\theta_3}\right) - \frac{k_2(a_1k_2\theta_2 - a_1\theta_2 + a_2k_1\theta_3)}{a_1\theta_2}\left(\frac{b\theta_1}{a_2\theta_3}\right)^2 + O\left(n_2^3\right). \tag{48}$$

3.2 Mass Action Calculations

Take the limit of the Michaelis-Menten equation when $x \ll k$, and rename $\frac{c}{k} \to w$. The equation becomes

$$1 - mx = wx \tag{49}$$

with $m, w, x \geq 0$, $x < 1$. This equation admits the nonnegative solution

$$p_{\mathrm{MA}}(w,m) = \frac{1}{m+w}. \tag{50}$$

The quantity $p_{\mathrm{MA}}(w,m)$ always lies between 0 and $1/m$, and is a decreasing function of w and m. For the three-sector model, we can express the fixed point solution as

$$Y_1^* = p_{\mathrm{MA}}\left(1, \frac{r_1\theta_2}{b\theta_1}\right) \equiv p_{\mathrm{MA}}(w_1, m_1), \tag{51a}$$
$$Y_2^* = p_{\mathrm{MA}}\left(\frac{b\theta_1}{r_1\theta_2}\frac{1}{Y_1^*}, \frac{r_2\theta_3}{r_1\theta_2}\frac{1}{Y_1^*}\right) \equiv p_{\mathrm{MA}}(w_2, m_2), \tag{51b}$$
$$Y_{k+2}^* = \theta_k W^*, \quad W^* \equiv 1 - Y_1^* - Y_2^*, \quad k = 1, 2, 3. \tag{51c}$$

Proposition 3.1.

(1) The function $p_{MM}(c, k, m)$ satisfies the rescaling relation

$$p_{MM}(c, k, m) = \frac{1}{m} p_{MM}(c, km, 1) \equiv \frac{1}{m}\Phi(c, km), \tag{52}$$

(2) The function $p_{MM}(c, k, m)$ satisfies the rescaling relation

$$p_{MM}(c, k, m) = k p_{MM}(c, 1, km) \equiv \frac{1}{m}\Psi(c, km), \tag{53}$$

(3) Rescaling p_{MM} by k and taking the limit $x \to 0$ gives p_{MA}.

Proof.

(1) Let $\xi = mx$, then

$$1 - \xi = \frac{c\,\xi}{km + \xi} \implies x = \frac{\xi}{m} = \frac{1}{m} p_{\mathrm{MM}}(c, km, 1).$$

(2) Let $\xi = x/k$, then

$$1 - km\xi = \frac{c\,\xi}{1 + \xi} \implies x = k\,\xi = k\,p_{\mathrm{MM}}(c, 1, km).$$

(3) Let $\xi = x/k$, then

$$1 - km\xi = \frac{c\,\xi}{1 + \xi} \to c\,\xi.$$

Hence, we have $p_{\mathrm{MA}}(m, w) \equiv k\,p_{\mathrm{MM}}(c, 1, km)$ when $x \ll 1$.

□

As shown in proposition 3.1, we can express the general solution to the n-partition model using the p_{MA} function. This will again help us in showing the system has a unique nonnegative fixed point.

$$\boxed{\begin{aligned} Y_1^* &= p_{\mathrm{MA}}\left(1, \frac{r_1\theta_2}{b\theta_1}\right), && \text{(54a)}\\ Y_i^* &= p_{\mathrm{MA}}\left(\frac{b\theta_1}{r_{i-1}\theta_i}\frac{1}{Y_{i-1}^*}, \frac{r_i\theta_{i+1}}{r_{i-1}\theta_i}\frac{1}{Y_{i-1}^*}\right), \quad i = 2, \ldots, n-1, && \text{(54b)}\\ Y_{k+n-1}^* &= \theta_k\left(1 - \sum_{i=1}^{k-1} Y_k^*\right), \quad k = 1, \ldots, n. && \text{(54c)} \end{aligned}}$$

4 Special Function Plots

A log-scale plot of the Michaelis-Menten special function $p_{\mathrm{MM}}(c,k,m)$ is shown in Figure 7 below, with $m=\frac{1}{2}$. We can see that as c increases, $p_{\mathrm{MM}}(c,k,m)$ increases from 0 to $\frac{1}{m}=2$. As k increases, $p_{\mathrm{MM}}(c,k,m)$ decreases for fixed c. This behavior is consistent with our earlier analysis.

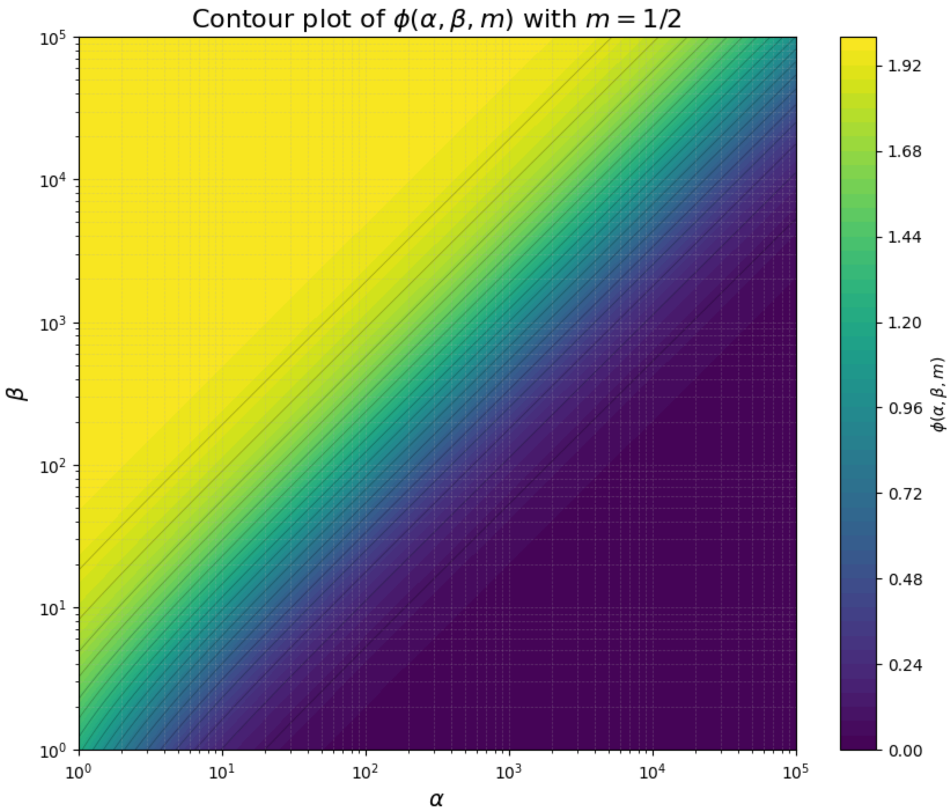

Figure 7: Plotted with $m=\frac{1}{2}$.

5 Overrabundance Limit for Three-Sector Model

In progress...

6 Bottleneck Limit for N-Sector Mass Action Model

In progress...