

THREE POOL MODEL FOR BACTERIAL GROWTH

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1. GENERAL IDEA

When a population of bacteria experiences a new environmental situation they often need time to adapt to the new situation. Some bacteria even may not be able to adjust and die other will enter the exponential growth phase after a lag phase. Motivated by this we divide a bacterial population into three pools:

- $L(t)$: the fraction of the population doing nothing - being in the lag phase
- $D(t)$: the fraction of the population undergoing cell death
- $G(t)$: the fraction of the population growing and dividing

2. NO BACK-FLOW FROM G AND D TO L

The pools G and D are unidirectionally connected with the pool L . We assume for simplicity that there is no link between G and L . The suggested model can be cast in the following two reactions:



The fraction G of the exponentially growing cells will go to steady state due to limitations in resources. λ is the rate by which cells go from the lag phase to the growth phase; μ is the rate by which cells go from the lag phase to the state in which they die; α is the growth rate of the healthy population; β is the rate by which the cells are removed from the D pool. Note that one could further simplify this model to a two pool or state model by omitting the pool D and removing cells with rate β directly from pool L . The relevant question here is whether cells in the pool D still contribute to the limitation of the resources by, e.g., occupying space or consuming important nutrients. If yes, the three pool model would be advantageous, if not the two pool model is sufficient with the advantages of having one parameter less.

The dynamics of the three pool model can be captured by the coupled system of ordinary

differential equations (the two pool model can be achieved by setting $D \equiv 0$ and replacing μ with β):

$$(6) \quad \dot{L} = -(\mu + \lambda)L$$

$$(7) \quad \dot{G} = \lambda L + \alpha G \left(1 - \frac{L + G + D}{N_t}\right) - \mu' G$$

$$(8) \quad \dot{D} = \mu L + \mu' G - \beta D$$

to be solved with the initial conditions $L(0) = n_0$, $G(0) = 0$, and $D(0) = 0$, where n_0 is the initial bacterial population. N_t denotes the maximal size of the total bacterial population due to environmental limitations. For $\mu' = 0$ the equations for L and D can be readily integrated resulting in:

$$(9) \quad L(t) = n_0 e^{-(\mu + \lambda)t}$$

$$(10) \quad D(t) = n_0 \mu e^{-\beta t} \frac{1 - e^{-(\mu + \lambda - \beta)t}}{\mu + \lambda - \beta}.$$

For constant parameters μ , λ , and β the integrals for L and D can be put into the differential equation for G . However, for time dependent parameters, e.g. for a dependence on a non-static, dynamic temperature, it appears to be not advantageous to use the analytical results for L and D and work instead with all three equations for L , G , and D . It is interesting to see what type of equations result for the total bacterial population $n = L + G + D$:

$$(11) \quad \dot{G} = \lambda L + \alpha G \left(1 - \frac{n}{N_t}\right)$$

$$(12) \quad \dot{n} = -\beta D + \alpha G \left(1 - \frac{n}{N_t}\right).$$

with the initial conditions $G(0) = 0$ and $n(0) = n_0$. These equations have a clear interpretation, are derived from simple principles, and are different from the popular Barayni-Roberts and modified-Gompertz models. A notable difference is that the growth rate α is time independent. For the functions L and D it holds: $\lim_{t \rightarrow \infty} L(t) = \lim_{t \rightarrow \infty} D(t) = 0$. It follows immediately that $\lim_{t \rightarrow \infty} G(t) = N_t$. The equation exhibit a lag phase and an initial drop due to cell death. To find a substantial initial drop one needs $\beta\mu \gg \alpha\lambda$. The lag time t_L can be approximated by the time at which half of the initial population is in the growth phase, i.e., $n_0 = 2G(t_L)$. Assuming $L \ll N_t$ we can ignore the non-linear term in the equation for G , which gives rise to:

$$(13) \quad 1 = 2 \int_0^{t_L} \lambda L(t) e^{\alpha(t_L - t)} dt$$

$$(14) \quad 1 = 2\lambda e^{\alpha t_L} \frac{1 - e^{-(\mu + \lambda + \alpha)t_L}}{\mu + \lambda + \alpha}.$$

For $\alpha > \mu + \lambda$ t_L can be approximated by:

$$(15) \quad t_L \approx -\frac{1}{\alpha} \ln \left(\frac{2\lambda}{\mu + \lambda + \alpha} \right).$$

The lag time t_L diverges very slowly, logarithmically with $\lambda \rightarrow 0$.

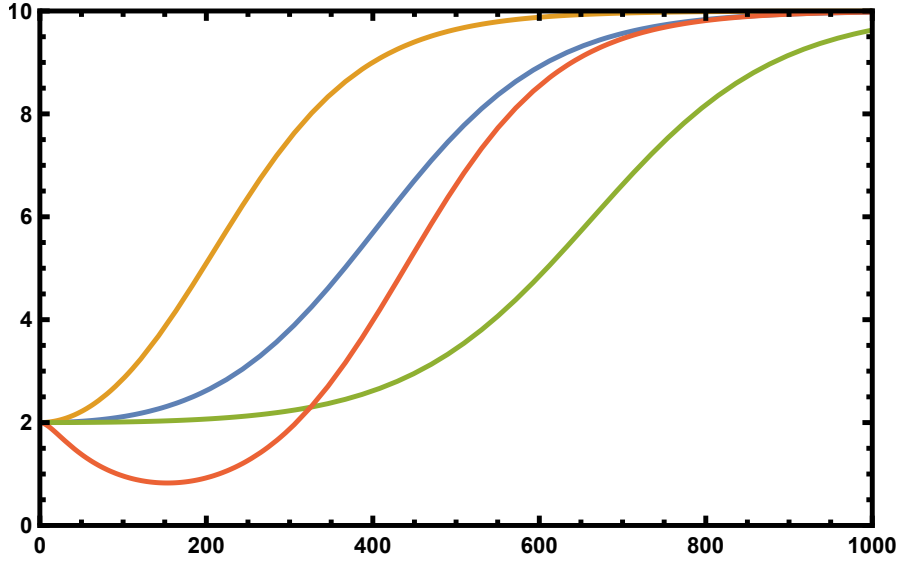


FIGURE 1. The dynamics of the sum of $n = L + G + D$, the size of the bacteria population. Short lag times, $\lambda = 10^{-2}$, orange curve. Intermediate lag time, $\lambda = 10^{-3}$, blue curve. Long lag time, $\lambda = 10^{-4}$, green curve. For all three curves $\mu = 0$ (no dying bacteria). Significant dip for intermediate lag time and dying bacteria, $\lambda = 10^{-3}$, $\mu = 10^{-2}$. The other parameters are the same for all curves and read: $\alpha = 1.1 \times 10^{-2}$, $\beta = 10^{-1}$, $n_0 = 2$, $N_t = 10$.

3. COMPARISON TO THE BARAYNI-ROBERTS MODEL

The equation for the Barayni-Roberts model is given by:

$$(16) \quad \dot{n} = \alpha(t)n \left(1 - \frac{n}{N_t}\right)$$

$$(17) \quad \alpha(t) = \alpha_m \frac{\rho e^{\nu t}}{1 + \rho e^{\nu t}}.$$

The initial and maximal are $\alpha(0) = \alpha_m \rho$ and $\lim_{t \rightarrow \infty} \alpha(t) = \alpha_m$. The parameters ρ and ν modulate the lag-phase. ρ should be sufficiently smaller than α_m to result in very small initial growth. However, the parameters ρ and ν lack a clear meaning. To compare this with the three-pool model one has to set $\mu = 0$, i.e., no dying bacteria ($D \equiv 0$). Because the total bacteria population n is $n = G + L$ we can write $G = n - L$ and with

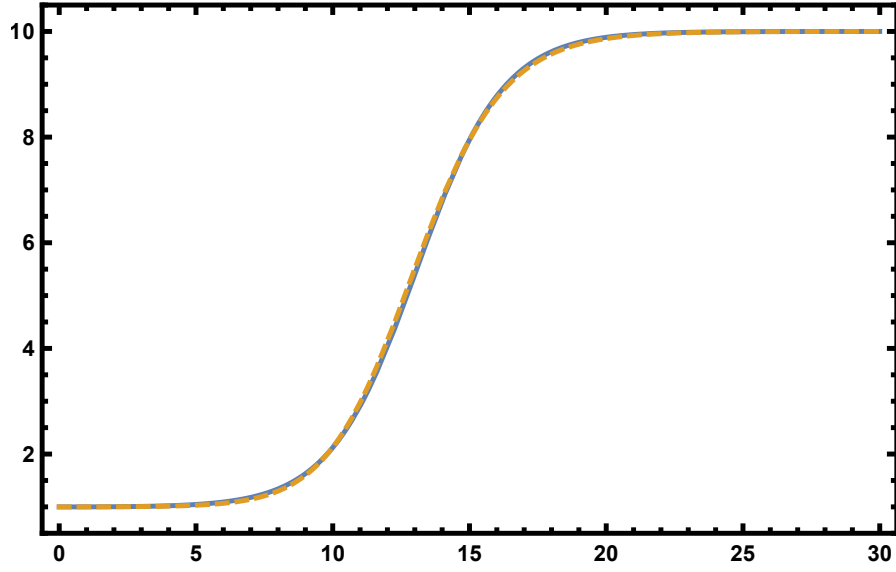


FIGURE 2. Comparison of the Barayni-Roberts model (dashed line) and the Three-Pool model (solid line). The parameters are $\alpha = 0.7$, $\lambda = 1.5^{-3}$, $\mu = 0$, $\beta = 0$, $N_t = 10$ for the Three-Pool Model and $\alpha = 0.588$, $\rho = 10^{-3}$, $\nu = 0.77$, $N_t = 10$ for the Barayni-Roberts model.

this we find (using $n(t=0) = n_0$ and $G(t=0) = 0$):

$$(18) \quad \dot{n} = \alpha G \left(1 - \frac{n}{N_t} \right)$$

$$(19) \quad \dot{n} = \alpha(n - L) \left(1 - \frac{n}{N_t} \right)$$

$$(20) \quad \dot{n} = \alpha \left(n - n_0 e^{-\lambda t} \right) \left(1 - \frac{n}{N_t} \right).$$

Notably, the pool model has a different structure and has one parameter less. All parameters can be given a clear meaning. Although the structure is different both models can produce the same results and in this sense they are equivalent as can be seen in Figure 2.

4. BACK-FLOW FROM G TO L

We explore now the idea that under certain conditions, as sudden change in the environment, part of the population G will enter a lag-phase, i.e., there is a back-flow

from G to L .

$$(21) \quad L \xrightarrow{\lambda} G$$

$$(22) \quad L \xrightarrow{\mu} D$$

$$(23) \quad G \xrightarrow{\alpha} 2G$$

$$(24) \quad G \xrightarrow{\gamma(t)} L$$

$$(25) \quad D \xrightarrow{\beta} \emptyset$$

The rate $\gamma(t)$ depends on the rate of change of the environment. Stronger and quicker changes will lead to a higher rate γ . Let the change in the environment be in temperature T .

4.1. Maxwell type of stress - strain relation. We propose a kind of visco-elastic Maxwell type of stress-strain relation and write down the ordinary differential equation for γ to be:

$$(26) \quad \dot{\gamma} = \Gamma \left| \dot{T} \right| - \delta \gamma.$$

We assumed that the direction of the temperature change does not matter, i.e., a change from $T = 2$ to $T = 12$ has the same effect as a change from $T = 14$ to $T = 4$. Γ is a scaling factor and δ is the relaxation time for the temperature disturbance. Integration of this equation yields (with $\gamma(0) = 0$):

$$(27) \quad \gamma(t) = \Gamma \int_0^t \left| \dot{T}(t') \right| e^{-\delta(t-t')} dt'.$$

After some manipulation of this equation we find:

$$(28) \quad \gamma(t) = \Gamma \delta \left[T[t] - T[0]e^{-\delta t} - \delta \int_0^t T(t')e^{-\delta(t-t')} dt' \right].$$

This representation of the rate $\gamma(t)$ has the advantage that it only involves $T(t)$ and does not require the calculation of the derivative of T . If T exhibits n temperature jumps, one finds:

$$(29) \quad \gamma(t) = \Gamma \sum_{i=1}^n |\Delta T_i| \theta(t - t_i) e^{-\delta(t-t_i)}.$$

The ordinary differential equations for the pool model with environmental-shock based back-flow read:

$$(30) \quad \dot{L} = \gamma(t)G - (\mu + \lambda)L$$

$$(31) \quad \dot{G} = \lambda L - \gamma(t)G + \alpha G \left(1 - \frac{L + G + D}{N_t} \right)$$

$$(32) \quad \dot{D} = \mu L - \beta D$$

This model has already seven parameters. The solution for one temperature jump of $\Delta T = 10$ at $t = 400$ is given in Figure 4.

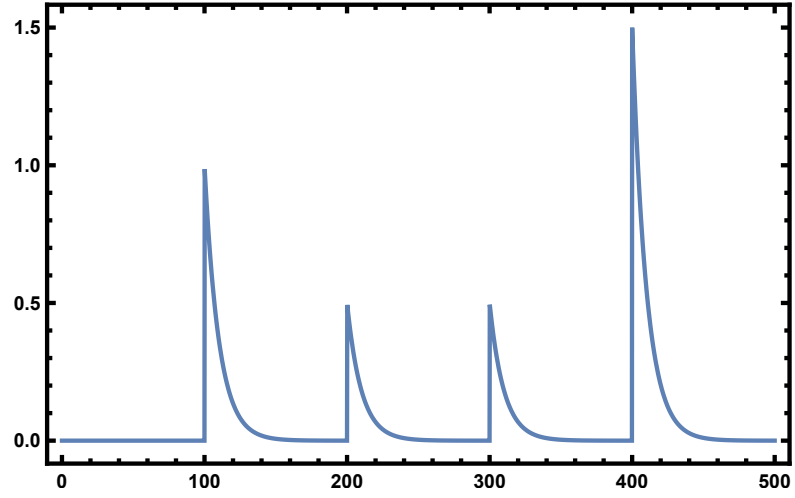


FIGURE 3. The back-flow rate γ , by which the growing bacterial population G goes back to the lag-phase population L . Shown is the rate γ for four temperature jumps at $t = 100, 200, 300, 400$ with the temperature difference $\Delta T = 10, 5, 5, 15$. The parameters are $\Gamma = 1$, $\delta = 0.1$.

4.2. Memory equation for the temperature stress -strain relation.

$$(33) \quad \dot{\gamma} = \int_{-\infty}^t M(t-t') \dot{T}(t') dt' - \delta \gamma.$$

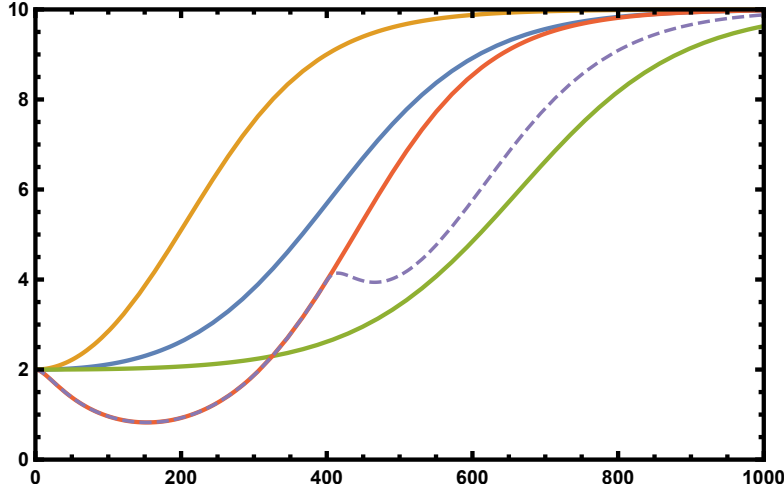


FIGURE 4. The dynamics of the sum of $n = L + G + D$, the size of the bacteria population. The curves are the same as in Figure 1, besides the dashed line. Short lag times, $\lambda = 10^{-2}$, orange curve. Intermediate lag time, $\lambda = 10^{-3}$, blue curve. Long lag time, $\lambda = 10^{-4}$, green curve. For all three curves $\mu = 0$ (no dying bacteria). Significant dip for intermediate lag time and dying bacteria, $\lambda = 10^{-3}$, $\mu = 10^{-2}$. Temperature shock, $\Delta T = 10$, for intermediate lag time and dying bacteria, $\lambda = 10^{-3}$, $\mu = 10^{-2}$, $\delta = 0.1$, dashed curve. The other parameters are the same for all curves and read: $\alpha = 1.1 \times 10^{-2}$, $\beta = 10^{-1}$, $n_0 = 2$, $N_t = 10$.

5. EXTENDING THE THREE POOL MODEL

In the previous sections the saturation of the growth pool G was achieved by using the logistic growth function. To base the TPM on elementary elements, we include several additional element.

5.1. Resource dependence. We aim to include a resource pool which is used by the growing bacteria. Once the pool is depleted the growth of the bacteria stops. The simplest way to include this is:

$$(34) \quad \dot{G} = \alpha_0 R G$$

$$(35) \quad \dot{R} = -\alpha_0 R G$$

Exploiting $R + G = \text{const} = C$ we find:

$$(36) \quad \dot{G} = \alpha_0 (C - G) G$$

$$(37) \quad \Leftrightarrow \dot{G} = \alpha_0 C \left(1 - \frac{G}{C}\right) G$$

Writing $\alpha := \alpha_0 C$ and $C = N_t$ this is of course the logistic growth equation. We insert this now into the simplest version of the TPM. To this end we assume that the bacteria only leave the lag-phase if there are nutrients, i.e., resources. Otherwise they stay in the

lag-phase:

$$(38) \quad \dot{L} = -\lambda RL$$

$$(39) \quad \dot{G} = \lambda RL + \alpha RG$$

$$(40) \quad \dot{R} = -\frac{\alpha}{N_t} RG$$

We rescaled R by N_t , such that it is dimensionless. One note about R : the pools L and G represent number of bacteria (or number of bacteria per unit area/volume) while R represents an abstract resource pool. Let say $G = N_B/V$ and $[G] = 1/V$, where N_B is number of bacteria and V is the volume. Then $R = N_R/V$ and $[R] = 1/V$, where N_R is the number of resource molecules (or any appropriate unit, e.g., mol). Then $[\alpha_0] = V/s$, $[N_t] = 1/V$, and $[\alpha] = 1/s$. For homogeneous densities it is equivalent to consider the total amount, i.e., multiplying L and G by the volume. In this case $[L] = [G] = [N_t] = 1$.

Turning back to the equations above we can state: $L + G + N_t R = N_t$. For $t = 0$ we have $n_0 + N_t R_0 = N_t$ (given $L_0 = n_0$ and $G_0 = 0$) and from this: $N_t R_0 = N_t - n_0$. Using this we eliminate R and arrive at:

$$(41) \quad \dot{L} = -\lambda \left(1 - \frac{L + G}{N_t}\right) L$$

$$(42) \quad \dot{G} = \lambda \left(1 - \frac{L + G}{N_t}\right) L + \alpha \left(1 - \frac{L + G}{N_t}\right) G$$

The steady state is $L_s + G_s = N_t$. However, it depends on the initial conditions and the parameters what L_s and G_s are. There is no way to determine L_s and G_s besides solving the dynamical equations, i.e., the steady state cannot be determined directly by solving a set of algebraic equations. To see this we determine the nullclines: the first nullcline is $G = N_t - L$ and the second is $G = N_t - L$, i.e., the nullclines coincides. Every point on the line $G = N_t - L$ is a fixed point. This can be seen in Fig. 5.

For $\lambda \ll \alpha$ the lag-pool is not emptied before all resources are consumed. As a consequence the lag-pool is non-zero in steady-state. In contrast, for $\lambda \gg \alpha$ the lag-pool is depleted before the resources are consumed, i.e., the lag-pool is zero in steady state.

5.2. Back-flow from the growth- to the lag-pool. The pool G represents the bacteria being in the metabolizing state. Once the resources are depleted the bacteria go back to the rest or lag-phase (needs to be checked). This can be modelled by:

$$(43) \quad \dot{L} = -\lambda_f RL + \mathcal{B}(R)G$$

$$(44) \quad \dot{G} = \lambda_f RL + \alpha RG - \mathcal{B}(R)G$$

$$(45) \quad \dot{R} = -\frac{\alpha}{N_t} RG$$

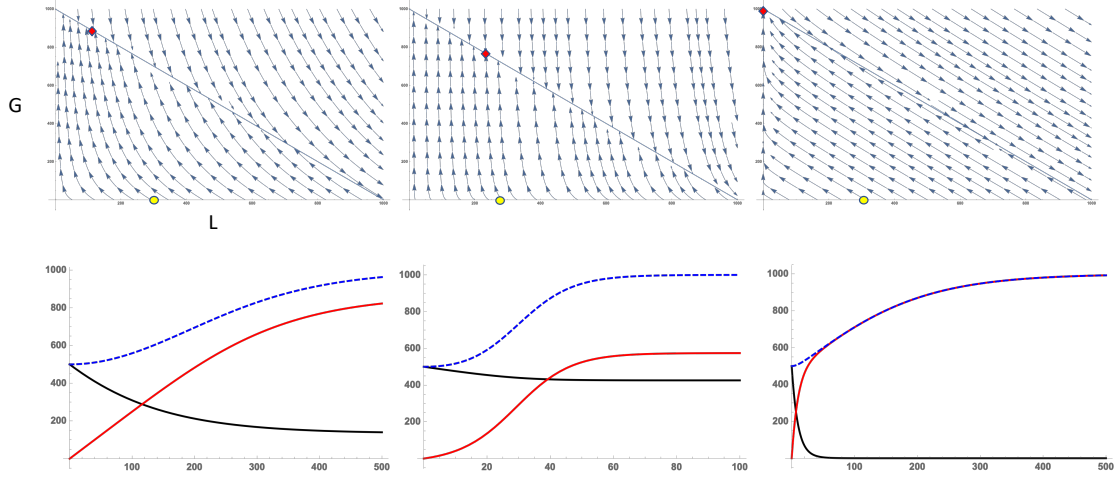


FIGURE 5. Upper panel: Phase portraits of the dynamics of the TPM with resource limitation. Abscissa: L and ordinate: G . Yellow circles indicate the initial condition, red Left: case $\lambda \approx \alpha$, $\lambda = 0.01$, $\alpha = 0.01$. Middle: case $\lambda \ll \alpha$, $\lambda = 0.01$, $\alpha = 0.2$. Right: case $\lambda \gg \alpha$, $\lambda = 0.2$, $\alpha = 0.01$. For all cases $G(t = 0) = 0$, $L(t = 0) = 500$, $N_t = 1000$. Lower panel: Dynamic of the pools L (black solid line), G (red solid line), and $T = G + L$ (blue dashed line).

The function \mathcal{B} captures how the bacteria go back to the lag-phase when resources are limited. Some simple choices:

$$(46) \quad \mathcal{B}_1 = \lambda_b$$

$$(47) \quad \mathcal{B}_2 = \frac{\lambda_b}{R^n}$$

$$(48) \quad \mathcal{B}_3 = \frac{\lambda_b K^n}{K^n + R^n}$$

$$(49) \quad \mathcal{B}_4 = \lambda_b \theta (K - R)$$

Note that \mathcal{B}_1 , \mathcal{B}_2 , and \mathcal{B}_4 are limiting case of \mathcal{B}_3 :

$$(50) \quad \mathcal{B}_1 = \lim_{K \rightarrow \infty} \mathcal{B}_3$$

$$(51) \quad \mathcal{B}_2 = \lim_{\substack{K \rightarrow 0 \\ \lambda_b K^n = \text{const}}} \mathcal{B}_3$$

$$(52) \quad \mathcal{B}_4 = \lim_{n \rightarrow \infty} \mathcal{B}_3$$

The parameter λ_b controls how quickly the bacteria go from the G to the L pool.

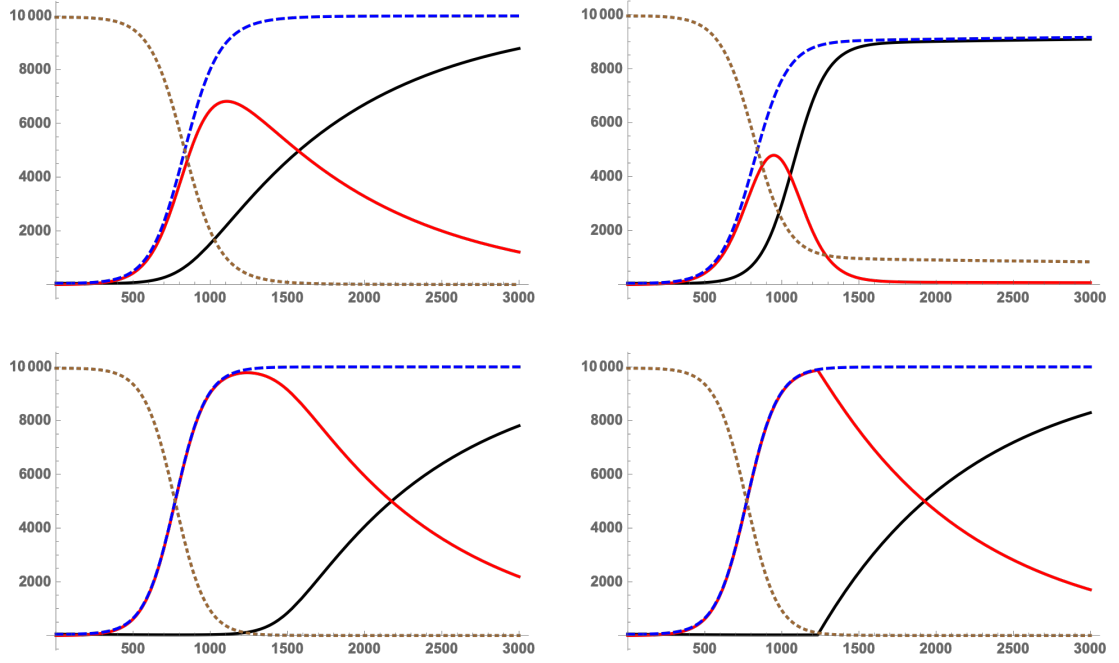


FIGURE 6. The dynamics of L (black solid line), G (red solid line), and $T = L + G$ (blue dashed line) for different back-flow models. The brown dashed line denotes the resource pool. Upper left: \mathcal{B}_1 , Upper right: \mathcal{B}_2 with $n = 1$. Lower Left: \mathcal{B}_3 with $K = 10^{-3}$, $n = 1$. Lower right: \mathcal{B}_4 with $K = 10^{-3}$. In all cases: $\lambda_b = 10^{-3}$, $\lambda_f = 10^{-3}$, $\alpha = 10^{-2}$, $L(0) = 50$, $G(0) = 0$, $N_t = 10^4$.

5.3. Waste production. The bacteria consume R and produce W . It is the accumulation of the bacteria waste which is responsible for the spoilage of food products. In order to take this into account we add an equation for the waste production:

$$(53) \quad \dot{L} = -\lambda_f RL + \mathcal{B}(R)G$$

$$(54) \quad \dot{G} = \lambda_f RL + \alpha RG - \mathcal{B}(R)G$$

$$(55) \quad \dot{R} = -\frac{\alpha}{N_t} RG$$

$$(56) \quad \dot{W} = \mathcal{F}(R, G).$$

The function \mathcal{F} denotes the model for the waste production rate. We shall discuss two possible models:

$$(57) \quad \mathcal{F}_1(R, G) = \kappa \alpha RG = -\kappa N_t \dot{R}$$

$$(58) \quad \mathcal{F}_2(R, G) = \kappa G$$

Model \mathcal{F}_1 results in waste accumulation in steady state $W_1^s = \lim_{t \rightarrow \infty} W_1(t) = \kappa(N_t - n_0)$. To see this we note $\dot{W}_1 = \kappa(\dot{L} + \dot{G})$, which yields: $W_1(t) = \kappa(L(t) + G(t) - n_0)$ where we used $W_1(0) = G(0) = 0$, $L(0) = n_0$. This model assumes that waste is only

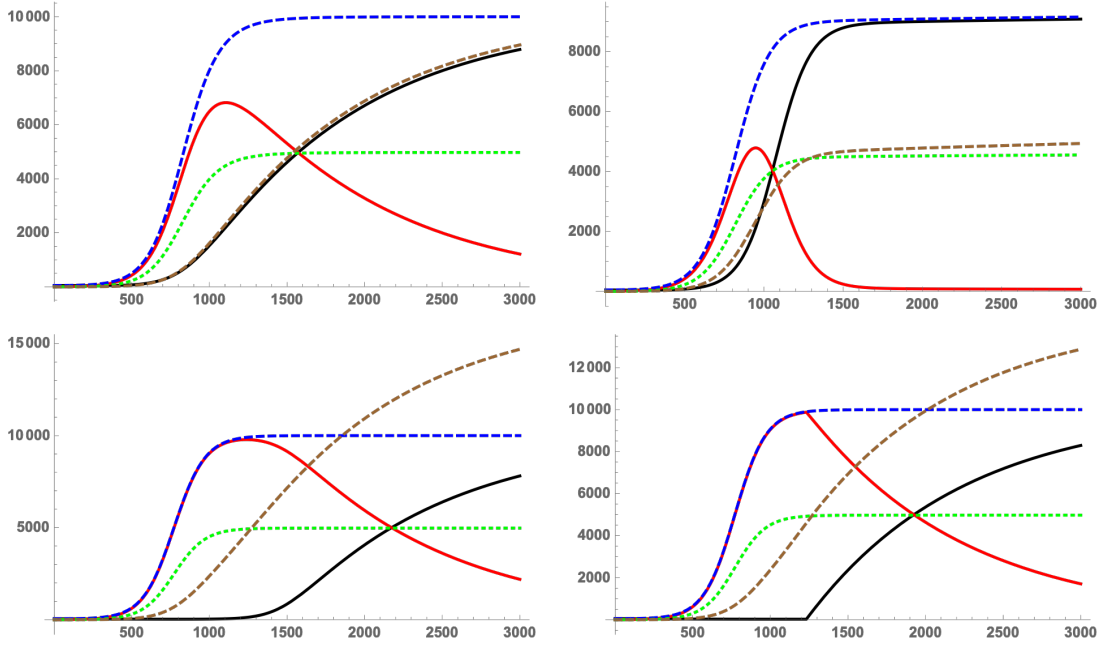


FIGURE 7. The dynamics of W_1 (green dotted line) and W_2 (brown dashed line). The other curves show L , G , and $T = L + G$ for different back-flow models as described in Fig. 6. $\kappa = 0.5$ for W_1 and $\kappa = 10^{-3}$ for W_2 .

produced when the bacteria grow and divide.

Model \mathcal{F}_2 results in $W_2(t) = \kappa \int_{t_0}^t G(t') dt'$. As long as $G > 0$ waste is produced, no matter whether the amount of bacteria is still growing. The amount of waste depends therefore on the back-flow model employed, which can be seen in Fig. 7.

5.4. Waste induced death. Potentially the waste of bacteria are harmful for themselves (or, e.g., the waste of bacteria A for bacteria B and vice versa). One can factor this in by:

$$(59) \quad \dot{L} = -\lambda_f RL + \frac{\lambda_b K^n}{K^n + R^n} G$$

$$(60) \quad \dot{G} = \lambda_f RL + \alpha RG - \frac{\lambda_b K^n}{K^n + R^n} G - \frac{\mu_W}{\kappa N_t} WG$$

$$(61) \quad \dot{R} = -\frac{\alpha}{N_t} RG$$

$$(62) \quad \dot{W}_1 = \kappa \alpha RG$$

$$(63) \quad \dot{W}_2 = \kappa G$$

We used model \mathcal{B}_3 for the back-flow and \mathcal{F}_2 for the waste production. This non-linear model exhibits already vast range of different dynamical behaviour.

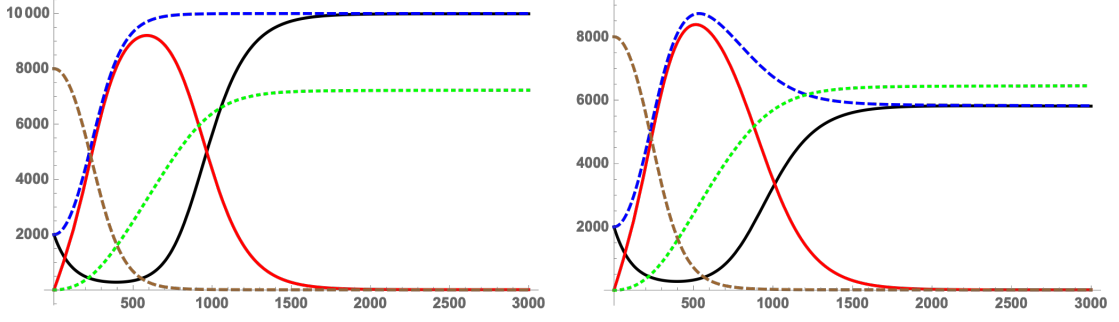


FIGURE 8. Difference of the dynamics without waste induced death (left) and with waste induced death (right) of the different pools: L (black solid line), G (red solid line), $L + G$ (blue dashed line), R (brown dashed line), and W (green dotted line). $L(0) = n_0$, $G(0) = 0$, $N_t R(0) = N_t - n_0$, $W(0) = 0$. $\lambda_b = 10^{-2}$, $\lambda_f = 10^{-2}$, $\alpha = 10^{-2}$, $K = 10^{-3}$, $N_t = 10^4$, $n_0 = 2000$. Left: $\mu_W = 0$, Right: $\mu_W = 2 \times 10^{-6}$.

6. INTERACTION BETWEEN BACTERIA

The TPM can be readily extended to more than one bacteria. Hereby is the interesting case that the bacteria interact via:

- Competition for common nutrients
- Influence by production of specific substances:
 - Mutual activation
 - Mutual inhibition

In general, a combination of these options will be the case. We will, however, focus on the discussion of the separate instances.

6.1. Competition for common nutrients. We consider for simplicity only one common resource pool. This stands either for one specific nutrient pool or subsumes all relevant nutrients. The simplest pool model for bacterial species A and B encompassing lag-phases, growth-phases and a common resource pool is given by (no back-flow to the lag-pool):

$$(64) \quad \dot{L}_A = -\lambda_A R L_A$$

$$(65) \quad \dot{L}_B = -\lambda_B R L_B$$

$$(66) \quad \dot{G}_A = \lambda_A R L_A + \alpha_A R G_A$$

$$(67) \quad \dot{G}_B = \lambda_B R L_B + \alpha_B R G_B$$

$$(68) \quad \dot{R} = -\frac{\alpha_A}{N_t} R G_A - \frac{\alpha_B}{N_t} R G_B$$

We again rescaled the resource pool with N_t and find

$$(69) \quad R = 1 - \frac{L_A + G_A + L_B + G_B}{N_t}$$

$$(70) \quad R_0 = 1 - \frac{n_A + n_B}{N_t}.$$

Inserting Eq. 69 into Eqs. 64 - 67 yields:

$$\dot{L}_A = -\lambda_A L_A + \frac{\lambda_A}{N_t} (L_A + G_A + L_B + G_B) L_A$$

$$\dot{L}_B = -\lambda_B L_B + \frac{\lambda_B}{N_t} (L_A + G_A + L_B + G_B) L_B$$

$$\dot{G}_A = \lambda_A L_A - \frac{\lambda_A}{N_t} (L_A + G_A + L_B + G_B) L_A + \alpha_A G_A - \frac{\alpha_A}{N_t} (L_A + G_A + L_B + G_B) G_A$$

$$\dot{G}_B = \lambda_B L_B - \frac{\lambda_B}{N_t} (L_A + G_A + L_B + G_B) L_B + \alpha_B G_B - \frac{\alpha_B}{N_t} (L_A + G_A + L_B + G_B) G_B$$

which has the structure of a generalised Lotka-Volterra system. In order to better see this, we set $L_A = L_B = 0$:

$$(71) \quad \dot{G}_A = \alpha_A G_A \left(1 - \frac{G_A}{N_t}\right) - \frac{\alpha_A}{N_t} G_A G_B$$

$$(72) \quad \dot{G}_B = \alpha_B G_B \left(1 - \frac{G_B}{N_t}\right) - \frac{\alpha_B}{N_t} G_A G_B.$$

For $N_t \gg \alpha_{A/B}$ the equations decouple. The null-clines of the system given by Eqs. 64 - 67 coincide and are given by $N_t = L_A + G_A + L_B + G_B$. If $\lambda_{A/B} > \alpha_{A/B}$ the lag-pools are completely depleted before the depletion of the resource pool stops the dynamics. To simplify the investigation of the systems dynamics we therefore ignore the L_A and L_B dimension and only consider the dynamics on the centre-manifold given by the $G_A \times G_B$ plane. The corresponding phase-plot is shown in Fig. 10. The advantage in using the pool model in contrast to using Lotka-Volterra directly is that all parameters have a clear meaning and consistent parameter relations arrive naturally. And a species can have more than one internal state. However, it is instructive to rewrite the system by setting $x_1 \equiv G_A$, $x_2 \equiv G_B$, and $\mathbf{x} = (x_1, x_2)^T$:

$$(73) \quad \dot{\mathbf{x}} = A\mathbf{x} + \frac{1}{2}\mathbf{x}B\mathbf{x}$$

$$(74) \quad A = \begin{bmatrix} \alpha_A & 0 \\ 0 & \alpha_B \end{bmatrix}$$

$$(75) \quad B = \frac{-2}{N_t} \begin{bmatrix} \alpha_A & \alpha_A \\ \alpha_B & \alpha_B \end{bmatrix}$$

The pool model, in contrast to the classical Lotka-Volterra approach, allows for far more flexibility. Non-linear functional responses can be introduced without any problem (see how section 7 for an extended discussion).

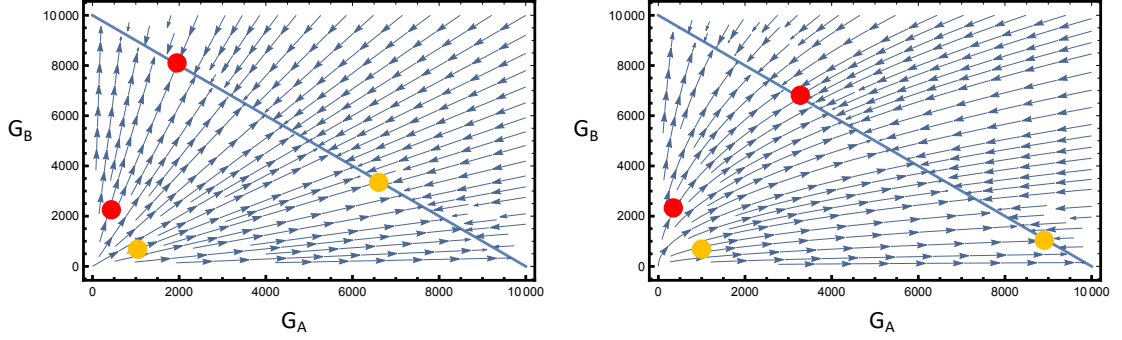


FIGURE 9. Phase portraits of the competition model given by Eqs. 71. Left: Equivalent species. The initial abundance decides about the steady state abundance. $\alpha_A = \alpha_B = 0.01$. Right: The growth rate of species A exceeds growth rate of species B, $\alpha_A = 0.01$, $\alpha_B = 0.005$. $N_t = 10^4$ in both cases.

6.2. Mutual inhibition. The simplest way to introduce inhibition of species A by species B is via a growth rate of species A depending on the abundance of species B. For sake of simplicity we ignore the lag pool and write for a mutual inhibition:

$$(76) \quad \dot{G}_A = \mathcal{B}_A(G_B)G_A \left(1 - \frac{G_A + G_B}{N_t}\right)$$

$$(77) \quad \dot{G}_B = \mathcal{B}_B(G_A)G_B \left(1 - \frac{G_A + G_B}{N_t}\right).$$

The function $\mathcal{B}_{A/B}$ captures the inhibiting effects in an effective way. It is straight forward to make the mechanism of inhibition more explicit by, e.g., introducing a waste pool. One possible choice for \mathcal{B} is:

$$(78) \quad \mathcal{B}(G) = \frac{\alpha}{1 + KG}.$$

This corresponds to the case $W \sim G$, where W is the waste (or whatever one chooses to call it) of species A affecting species B. If the waste accumulates one needs to replace G by $\int G dt$. Keeping it simple yields:

$$(79) \quad \dot{G}_A = \frac{\alpha_A G_A}{1 + K_B G_B} \left(1 - \frac{G_A + G_B}{N_t}\right)$$

$$(80) \quad \dot{G}_B = \frac{\alpha_B G_B}{1 + K_A G_A} \left(1 - \frac{G_A + G_B}{N_t}\right).$$

One can distinguish two limiting cases: *i)* $K_{A/B} \ll N_t$ and *ii)* $K_{A/B} \gg N_t$. In the first case the inhibition is of minor importance and could be ignored. In the latter case one

can simplify the equations, given n_A and n_B are non-zero:

$$(81) \quad \dot{G}_A = \tilde{\alpha}_A \frac{G_A}{G_B} (1 - G_A - G_B)$$

$$(82) \quad \dot{G}_B = \tilde{\alpha}_B \frac{G_B}{G_A} (1 - G_A - G_B).$$

We introduced the rescaled growth rates $\tilde{\alpha}_A = \alpha_A/(N_t K_B)$ and $\tilde{\alpha}_B = \alpha_B/(N_t K_A)$. Note that $[\tilde{\alpha}] = s^{-1}$. Rescaling time with $\tilde{\alpha}_A$ and defining the dimensionless parameter

$$(83) \quad \psi = \tilde{\alpha}_B / \tilde{\alpha}_A$$

$$(84) \quad \psi = \frac{K_B \alpha_B}{K_A \alpha_A}$$

results in:

$$(85) \quad \dot{G}_A = \frac{G_A}{G_B} (1 - G_A - G_B)$$

$$(86) \quad \dot{G}_B = \psi \frac{G_B}{G_A} (1 - G_A - G_B).$$

We can separate three cases:

$$(87) \quad \psi > 1 : \quad \text{Species B growth faster and/or inhibits A stronger}$$

$$(88) \quad \psi = 1 : \quad \text{A and B are equivalent}$$

$$(89) \quad \psi < 1 : \quad \text{Species A growth faster and/or inhibits B stronger}$$

6.3. Mutual activation/Mutuality. In case of mutual activation each of the two species benefit from the presence of the other. For sake of clarity we omit again the lag pool and write:

$$(90) \quad \dot{G}_A = \mathcal{B}_A(W_B, R) G_A$$

$$(91) \quad \dot{G}_B = \mathcal{B}_B(W_A, R) G_B$$

$$(92) \quad \dot{R} = -\mathcal{B}_A(W_B, R) G_A - \mathcal{B}_B(W_A, R) G_B$$

$$(93) \quad \dot{W}_A = \mathcal{F}_A(R, G_A)$$

$$(94) \quad \dot{W}_B = \mathcal{F}_B(R, G_B).$$

W_A and W_B denote the substance produced by species A and B, respectively. The functions $\mathcal{B}_A(W_B, R)$ and $\mathcal{B}_B(W_A, R)$ capture the resource dependent growth. Setting $\mathcal{B}_A(W_B, R) = \alpha_A W_B R$, $\mathcal{B}_B(W_A, R) = \alpha_B W_A R$, $\mathcal{F}_A(R, G_A) = \kappa_A R G_A$, $\mathcal{F}_B(R, G_B) = \kappa_B R G_B$, rescaling G_A , G_B , and W_B with N_t , W_A with κ_A/α_A , time with $\alpha_A N_t^2$, defining $\phi = \kappa_A \alpha_B / (\alpha_A^2 N_t)$, and $\psi = \kappa_B / (\alpha_A N_t)$ results in:

$$(95) \quad \dot{G}_A = W_B G_A (1 - G_A - G_B)$$

$$(96) \quad \dot{G}_B = \phi W_A G_B (1 - G_A - G_B)$$

$$(97) \quad \dot{W}_A = G_A (1 - G_A - G_B)$$

$$(98) \quad \dot{W}_B = \psi G_B (1 - G_A - G_B).$$

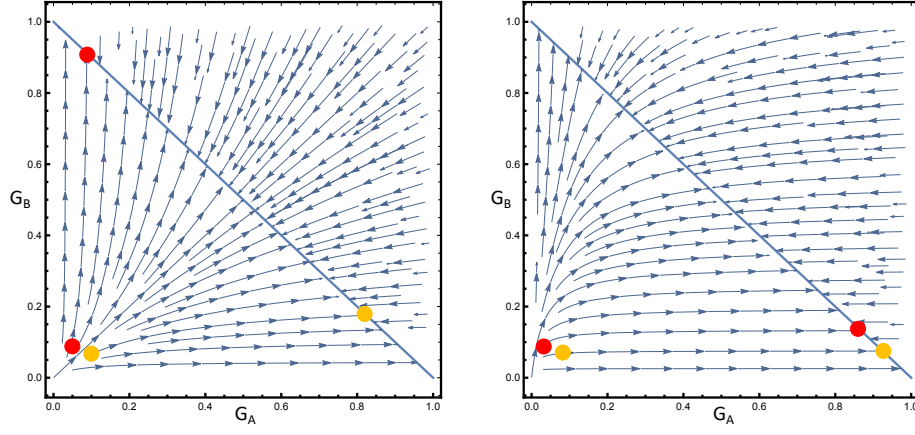


FIGURE 10. Simplified mutual inhibition model given by Eqs. 81. Left: Both species are equivalent, $\psi = 1$. Right: Species A exceeds (growth faster and/or suppresses stronger) species B, $\psi = 10$.

7. THE TPM AS A GENERALISED *generalised Lotka-Volterra model*