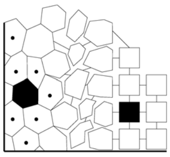
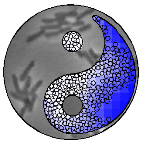


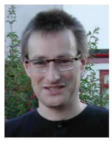


www.theobio.uni-bonn.de

Biofilms promote altruism

Jan-Ulrich Kreft[*]

Theoretical Biology, University of Bonn, Germany



Questions

- ➢ How can cooperative or altruistic behaviour evolve despite the fitness costs?
- ➢ How can a weaker competitor coexist with a stronger competitor?
- ➢ How fast should a bacterium grow?

These fundamental questions may at first appear unrelated, but a trade-off between growth rate and growth yield gives answers for all of them.

The trade-off: rate versus yield

The trade-off between growth rate and growth yield is based on irreversible thermodynamics which postulates a linear relationship between flux (proportional to growth rate) and thermodynamic force (proportional to energy dissipation). Higher growth rate means more energy has to be dissipated rather than converted to ATP, implying a lowered yield.

The existence of the trade-off provides an evolutionary choice between alternative survival strategies:

- ➢ High growth rate strategy (implies low yield)
- ➢ High growth yield strategy (implies slow growth)

Having a high yield of biomass per amount of substrate used means that resources are used economically.

Economic resource use benefits all those sharing the resource (the neighbours) while fast growth benefits the individual. This is known as the 'Tragedy of the commons' in our human context.

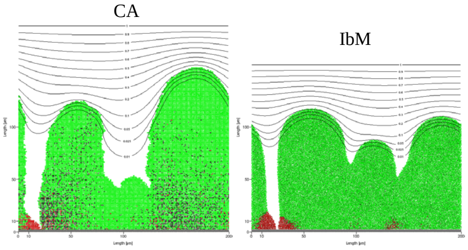
Economic resource use is a case of altruism, by definition: Altruistic behaviour benefits others more than self (fitness is relative and local, i.e, others are often not everyone but just a group, like all neighbours).

The model

BacSim is:

- ➢ individual-based: each bacterium has own state etc.
- ➢ 2D (essentially)
- ➢ multi-species (multi-substrate not used here)
- ➢ fully quantitative
- ➢ spatially structured (this is vital of course)
- ➢ bacteria are spheres in continuous space
- ➢ bacteria maintain a minimal distance to the neighbours by shoving them away when they get too close due to growth or cell division
- ➢ substrate diffusion and reaction as well as growth and spreading of cells are the only processes modelled

For cooperation and competition with neighbours, the most relevant feature of the the various biofilm models is the way biomass is spread because it affects the extent of mixing of clonal clusters in the biofilm, e.g., compare a CA model with the IbM BacSim:



The IbM preserves the clonality while the CA mixes the red and green species. NB: these bacteria are immotile.

[*] Contact: Jan-Ulrich Kreft, Theoretische Biologie, Universität Bonn, Kirschallee 1, D-53115 Bonn, Germany
kreft@uni-bonn.de
www.theobio.uni-bonn.de/people/jan_kreft

The competitors

We let two strategies compete (against each other and self):

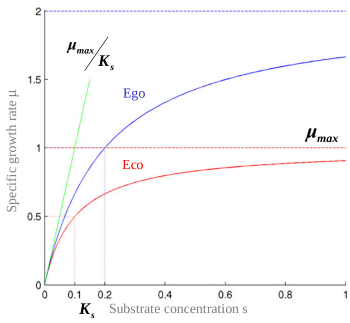
- Ego: high growth rate at low yield (Egoistic behaviour)
- Eco: high growth yield at low rate (Economy of resource use)

Strategy		Ego	Eco
Specific growth rate	$\mu = \frac{1}{x}\frac{dx}{dt}$	2	1
Yield coefficient	$Y_s = -\frac{dx}{ds}$	½	1
Energy dissipation	$-\Delta G^{\circ'}_{Diss}$	2	1
Specific substrate consumption rate	$-\frac{1}{x}\frac{ds}{dt} = \frac{\mu}{Y_s}$	4	1

These values were taken from measurements of *Holophaga foetida*, which can switch its metabolism from high to low ATP yield, according to growth conditions (Kappler *et al*. 1997).

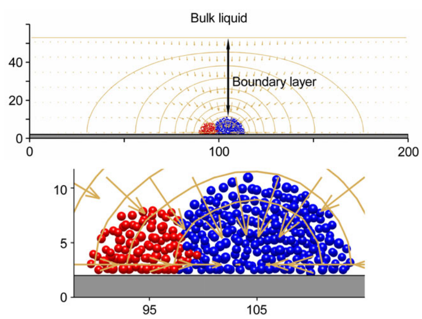
These two strategies differ regarding yield and growth rate, which is proportional to substrate concentration until it saturates at high substrate concentrations as described by Monod kinetics:

$$\mu = \mu_{\max} \frac{s}{K_s + s}$$



The pitch

Competition takes place in a biofilm setting where substrate gradients form due to the growth and activity of the biofilm bacteria. Note that due to substrate diffusing down from the bulk liquid above, whoever is at the top, receives more substrate and will grow better, a positive feedback loop.



Results

Chemostat

Ego always wins due to the higher growth rate over the whole range of substrate concentrations.

Biofilm

➢ Pure biofilms

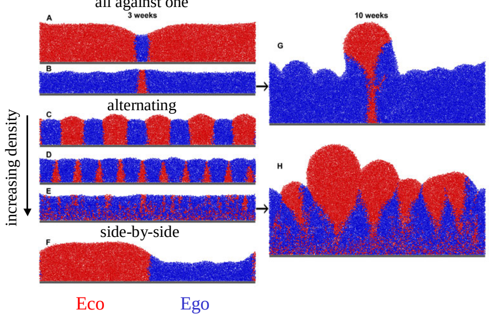
Ego grows faster initially, during the phase of exponential, unlimited growth. Later, substrate limitation gives Eco the long-term advantage.

➢ Mixed biofilms: Ego and Eco side-by-side

Similar to pure biofilms, Eco wins in the end, independent of density

➢ Mixed biofilms: Ego and Eco alternating

With increasing initial density of cells, Ego's faster growth during substrate abundance increases its chance to overgrow Eco. Once overgrown, the match is over (truncation selection).

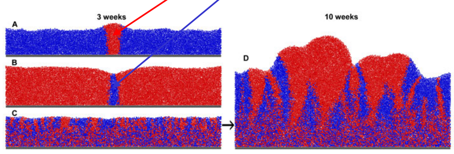


➢ Invasion of Ego biofilms by Eco and *vice versa*

Eco cells cannot invade Ego biofilms, but Eco groups can.

Ego cells can invade Eco biofilms, but Ego groups cannot.

Starting with a 50:50 random mixture, Eco wins due to a 'clustering effect': cell division of immotile cells leads to formation of clusters, or order, from chaos.



Conclusions

- ➢ Biofilms promote altruism
- ➢ Chemostat competition does not predict outcome in biofilms and nature
- ➢ Yield matters

Predictions

- ➢ Eco biofilms have higher surface area coverage
- ➢ Eco needs to grow in clusters and stick to self rather than mix (no twitching or other motility)
- ➢ This is why biofilms are typically composed of microcolonies
- ➢ Shedding of single cells from clusters is a purification step that is required for the survival of Eco strategists

References

Kappler O, Janssen PH, Kreft JU, Schink B (1997). Effects of alternative methyl group acceptors on the growth energetics of the O-demethylating anaerobe *Holophaga foetida*. Microbiology **143**: 1105-1114

Kreft JU, Picioreanu C, Wimpenny JWT, van Loosdrecht MCM (2001). Individual-based modelling of biofilms. Microbiology **147**: 2897-2912