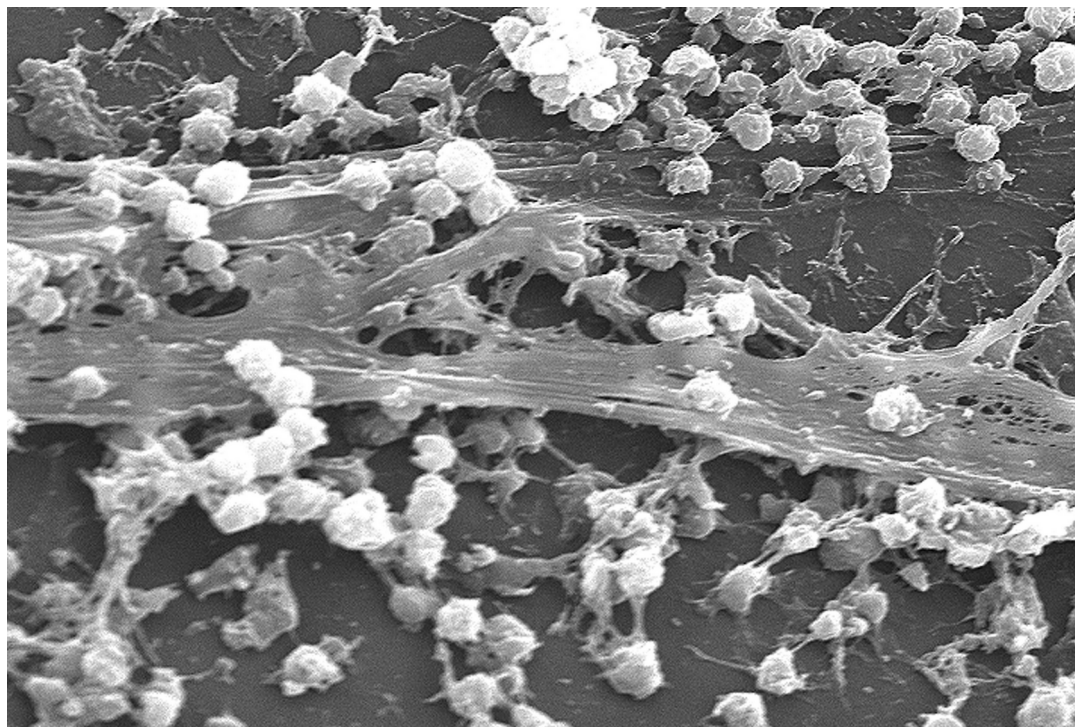


# **7. Competition, cooperation and spatial structure**

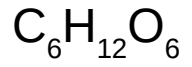
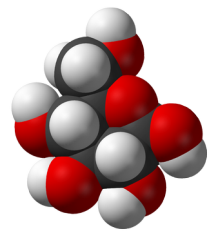
# Bacteria (often) live in a highly structured world → why does it matter?



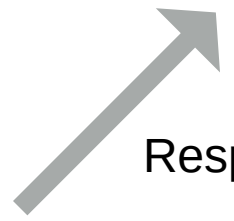
- **Competition** (for space or resources) is **local**
- **Interactions between individuals** (eg production of public good or bioweapons, signaling, etc) → Fitness of an individual depends on its neighbours

# Competition for resources: r/K selection

What to make from this glucose?

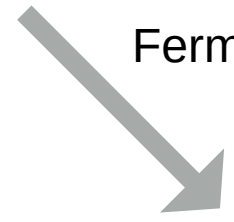


$$\frac{dN}{dt} = r * N * \left(1 - \frac{N}{K}\right)$$



Respiration

high K, low r  
(= 36 ATP, slow)



Fermentation

high r, low K  
(= 2 ATP, fast)

Trade-off between rate and yield: **Which one is selected?**

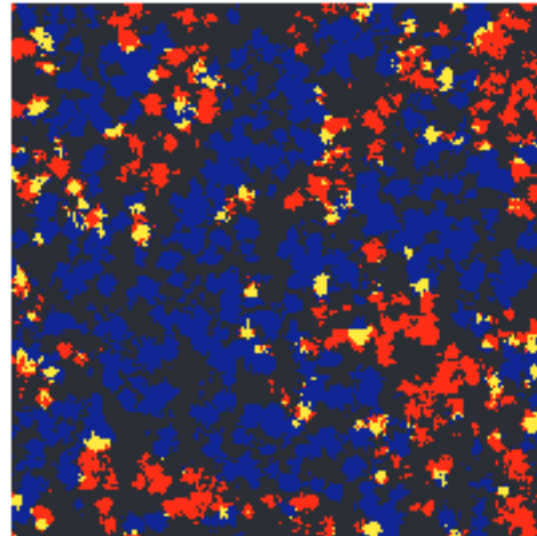
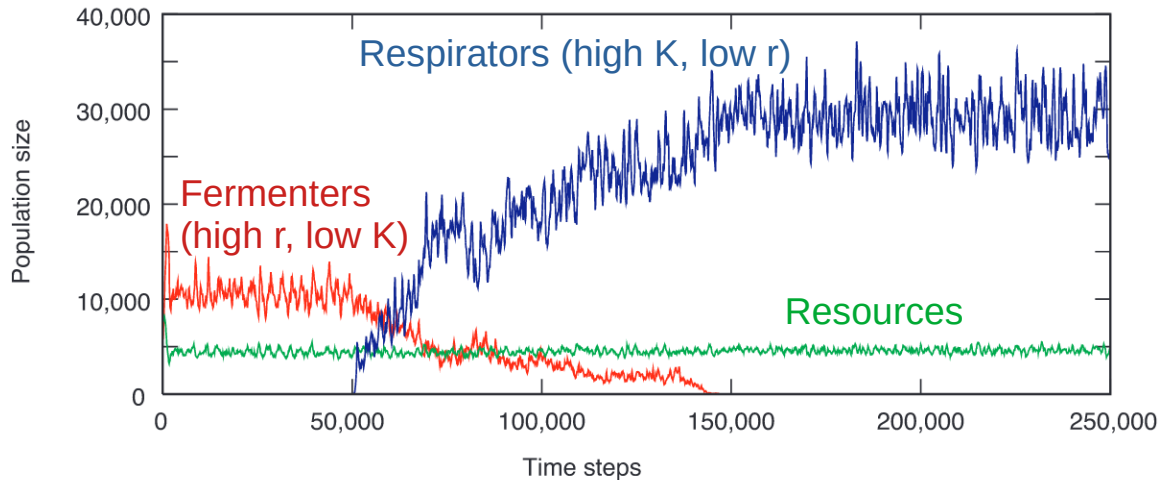
# Growing fast or efficiently: who wins?

- No space (mixed)? Both populations share the same  $K$ , but  $r$  is *private* → **Fermenters always win** (higher  $r$ )

$$\frac{dN_f}{dt} = r_f * N_f * \left(1 - \frac{N_f + N_r}{K_{(N_f, N_r)}}\right)$$

$$\frac{dN_r}{dt} = r_r * N_r * \left(1 - \frac{N_f + N_r}{K_{(N_f, N_r)}}\right)$$

- With space? → **Respirators** may win (we'll try to understand why)  
Pfeiffer, Schuster & Bonhoeffer, 2001



# Cooperative dilemma in biology

Type C = cooperate (pay a personal cost to bring a benefit to others)

Type D = do not cooperate (but can still benefit from cooperative act of others)

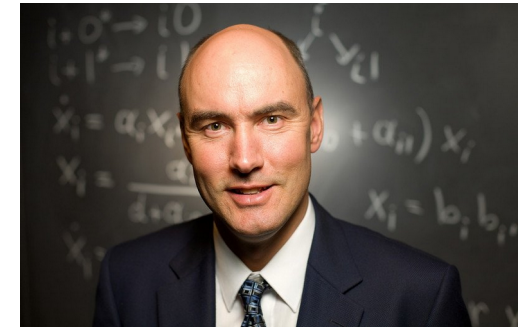
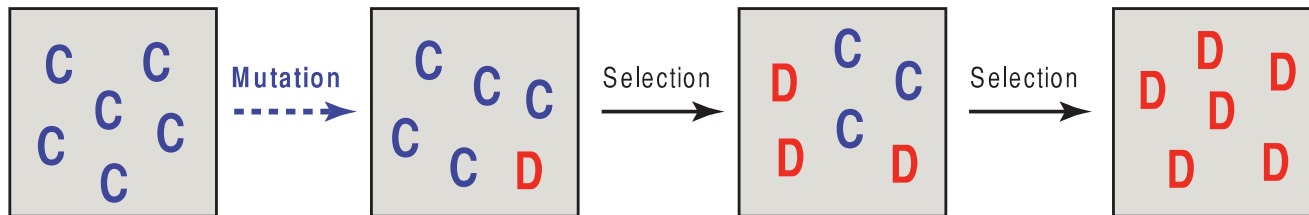
	C	D
C	R	S
D	T	P

Prisoner dilemma:  
 $T > R > P > S$  and  $R > (T+S)/2$

Pareto optimal

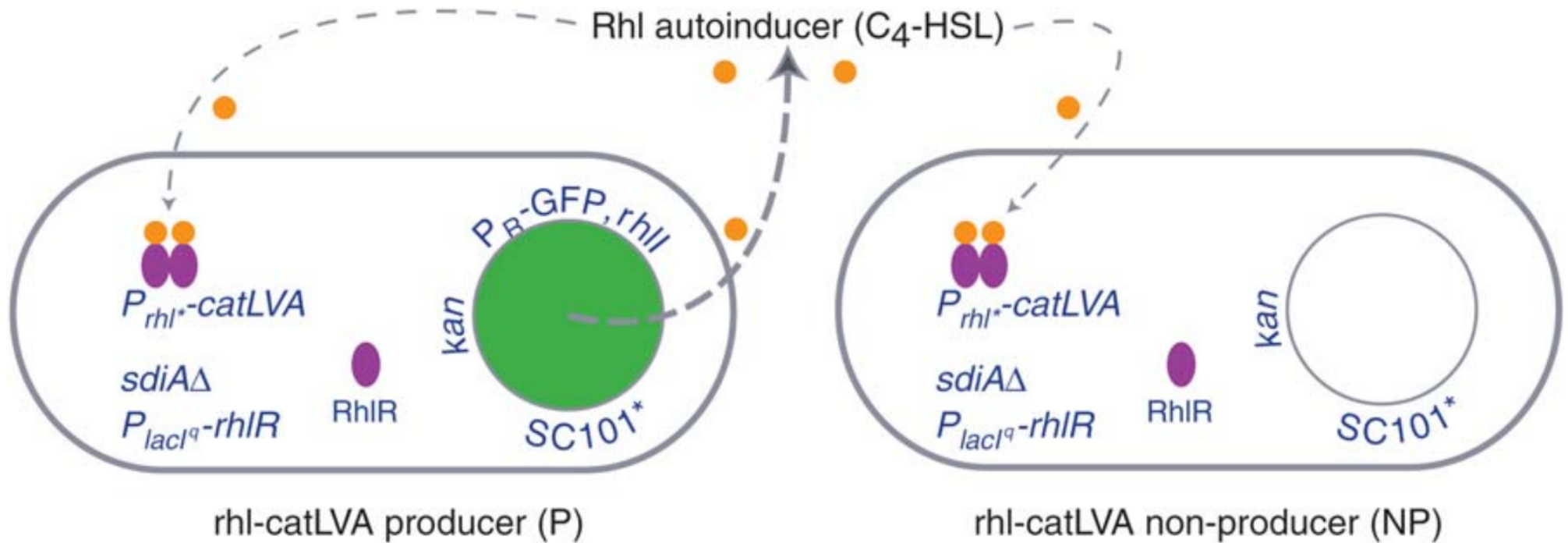
Nash equilibrium, ESS

Switching from type C to D always increase fitness → selection for type D **in mixed populations**



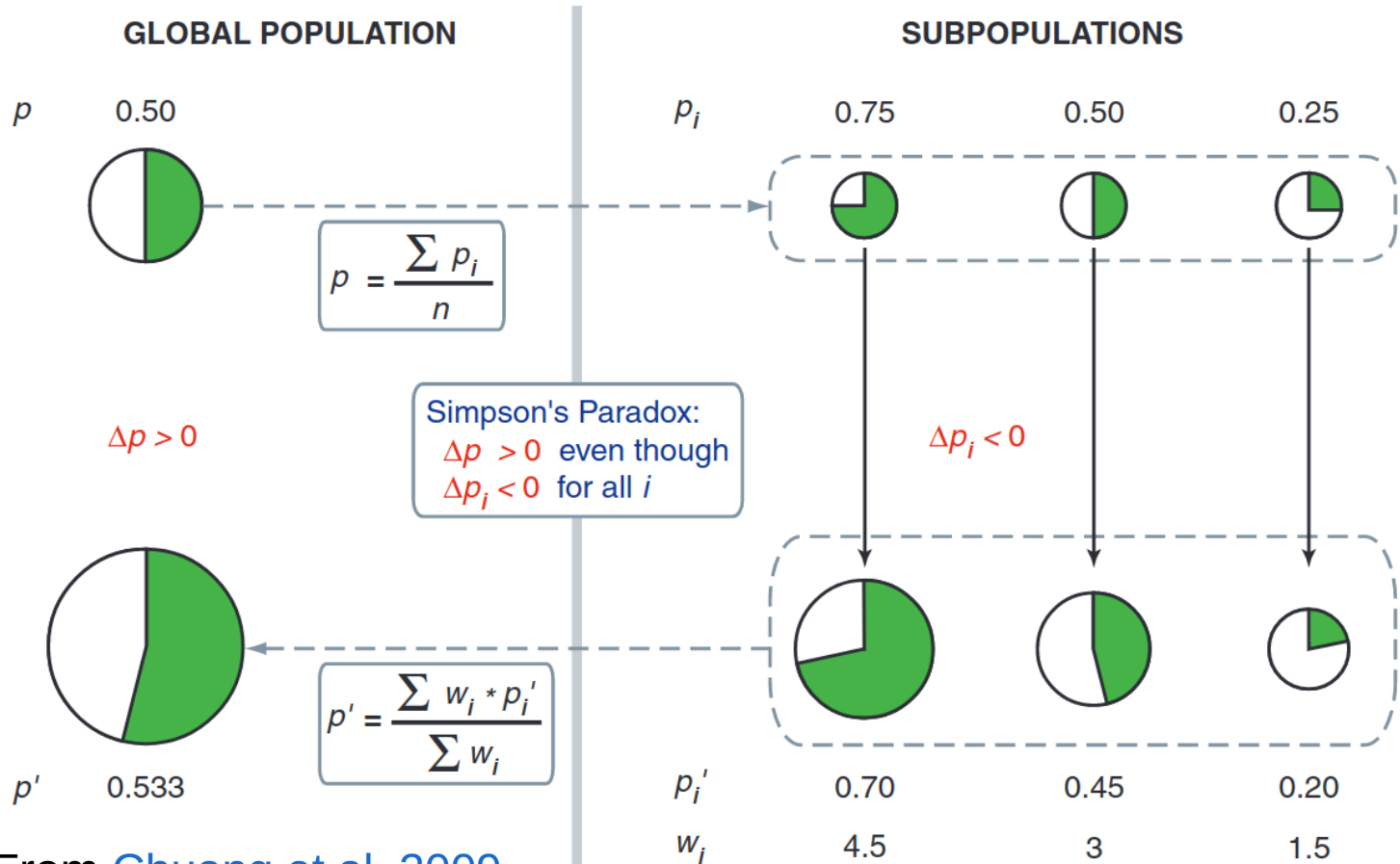
From [Nowak, 2006](#)

# Cooperative dilemma in isolated groups: Simpson paradox



Chuang et al, 2009: experiment with bacteria,  
with a synthetic *social* antibiotic resistance trait

# Cooperative dilemma in isolated groups: Simpson paradox



Within each group, cooperators *lose*

**But with spatial structure:**

groups of cooperators do better than group of non-cooperators

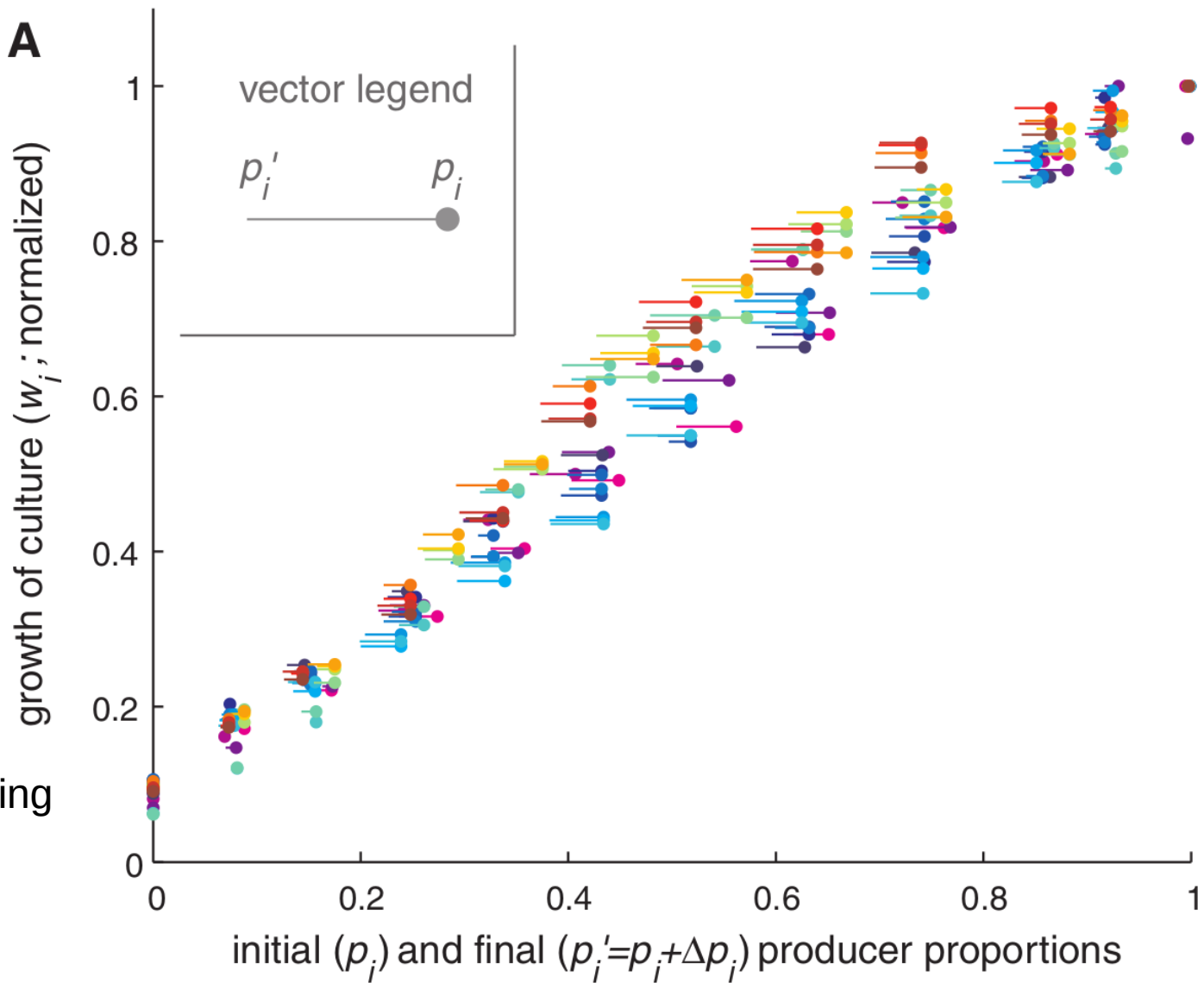
→ cooperation may increase overall

## The data: experimental proof of concept



Stan Leibler, one of the founding fathers of system biology

From [Chuang et al, 2009](#)





# General theory for the evolution of social traits

**Individuals of the same types  
interact more often**

Two frameworks to understand this:  
kin selection and group selection,  
Heated argument between proponents  
of each...

[Published: 26 August 2010](#)

## **The evolution of eusociality**

[Martin A. Nowak](#) , [Corina E. Tarnita](#) & [Edward O. Wilson](#)

[Nature](#) **466**, 1057–1062 (2010) | [Cite this article](#)

[Published: 23 March 2011](#)

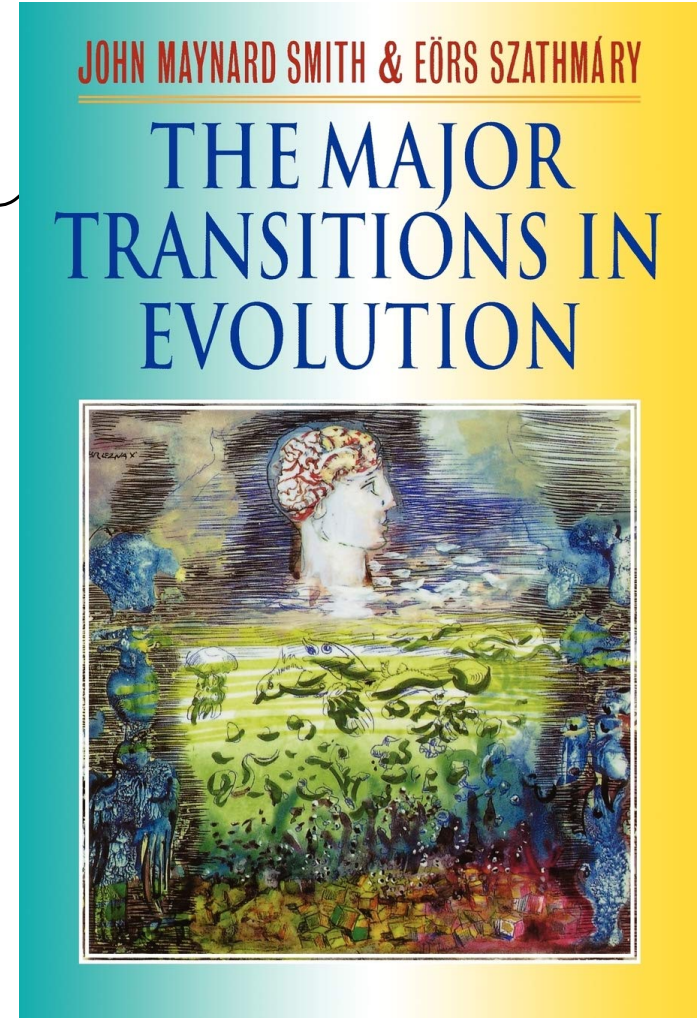
## **Inclusive fitness theory and eusociality**

[Patrick Abbot](#), [Jun Abe](#), [John Alcock](#), [Samuel Alizon](#), [Joao A. C. Alpedrinha](#), [Malte Andersson](#), [Jean-Baptiste Andre](#), [Minus van Baalen](#), [Francois Balloux](#), [Sigal Balshine](#), [Nick Barton](#), [Leo W. Beukeboom](#), [Jay M. Biernaskie](#), [Trine Bilde](#), [Gerald Borgia](#), [Michael Breed](#), [Sam Brown](#), [Redouan Bshary](#), [Angus Buckling](#), [Nancy T. Burley](#), [Max N. Burton-Chellew](#), [Michael A. Cant](#), [Michel Chapuisat](#), [Eric L. Charnov](#), [Tim Clutton-Brock](#), [Andrew Cockburn](#), [Blaine J. Cole](#), [Nick Colegrave](#), [Leda Cosmides](#), [Iain D. Couzin](#), [Jerry A. Coyne](#), [Scott Creel](#), [Bernard Crespi](#), [Robert L. Curry](#), [Sasha R. X. Dall](#), [Troy Day](#), [Janis L. Dickinson](#), [Lee Alan Dugatkin](#), [Claire El Mouden](#), [Stephen T. Emlen](#), [Jay Evans](#), [Regis Ferriere](#), [Jeremy Field](#), [Susanne Foitzik](#), [Kevin Foster](#), [William A. Foster](#), [Charles W. Fox](#), [Juergen Gadau](#), [Sylvain Gandon](#), [Andy Gardner](#), [Michael G. Gardner](#), [Thomas Getty](#), [Michael A. D. Goodisman](#), [Alan Grafen](#), [Rick Grosberg](#), [Christina M. Grozinger](#), [Pierre-Henri Gouyon](#), [Darryl Gwynne](#), [Paul H. Harvey](#), [Ben J. Hatchwell](#), [Jürgen Heinze](#), [Heikki Helanterä](#), [Ken R. Helms](#), [Kim Hill](#), [Natalie Jiricny](#), [Rufus A. Johnstone](#), [Alex Kacelnik](#), [E. Toby Kiers](#), [Hanna Kokko](#), [Jan Komdeur](#), [Judith Korb](#), [Daniel Kronauer](#), [Rolf Kümmerli](#), [Laurent Lehmann](#), [Timothy A. Linksvayer](#), [Sébastien Lion](#), [Bruce Lyon](#), [James A. R. Marshall](#), [Richard McElreath](#), [Yannis Michalakis](#), [Richard E. Michod](#), [Douglas Mock](#), [Thibaud Monnin](#), [Robert Montgomerie](#), [Allen J. Moore](#), [Ulrich G. Mueller](#), [Ronald Noë](#), [Samir Okasha](#), [Pekka Pamilo](#), [Geoff A. Parker](#), [Jes S. Pedersen](#), [Ido Pen](#), [David Pfennig](#), [David C. Queller](#), [Daniel J. Rankin](#), [Sarah E. Reece](#), [Hudson K. Reeve](#), [Max Reuter](#), [Gilbert Roberts](#), [Simon K. A. Robson](#), [Denis Roze](#), [Francois Rousset](#), [Olav Rueppell](#), [Joel L. Sachs](#), [Lorenzo Santorelli](#), [Paul Schmid-Hempel](#), [Michael P. Schwarz](#), [Tom Scott-Phillips](#), [Janet Shellmann-Sherman](#), [Paul W. Sherman](#), [David M. Shuker](#), [Jeff Smith](#), [Joseph C. Spagna](#), [Beverly Strassmann](#), [Andrew V. Suarez](#), [Liselotte Sundström](#), [Michael Taborsky](#), [Peter Taylor](#), [Graham Thompson](#), [John Tooby](#), [Neil D. Tsutsui](#), [Kazuki Tsuji](#), [Stefano Turillazzi](#), [Francisco Úbeda](#), [Edward L. Vargo](#), [Bernard Voelkl](#), [Tom Wenseleers](#), [Stuart A. West](#) , [Mary Jane West-Eberhard](#), [David F. Westneat](#), [Diane C. Wiernasz](#), [Geoff Wild](#), [Richard Wrangham](#), [Andrew J. Young](#), [David W. Zeh](#), [Jeanne A. Zeh](#) & [Andrew Zink](#) [-Show fewer authors](#)

[Nature](#) **471**, E1–E4 (2011) | [Cite this article](#)

# Examples of cooperative traits, in microbes and others

- Secretion of **public good** molecules (extra-cellular enzymes digesting a sugar or degrading an antibiotic, biofilm matrix...)
- Prudent use of resources
- Altruistic suicide
- Eusociality in animal societies
- Existence of multicellular organisms by itself



# Cooperation and selfish

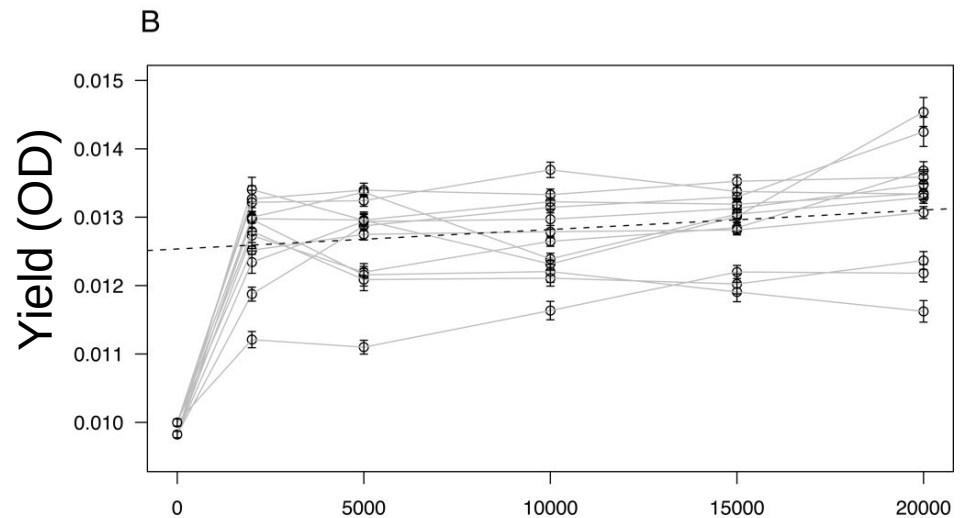
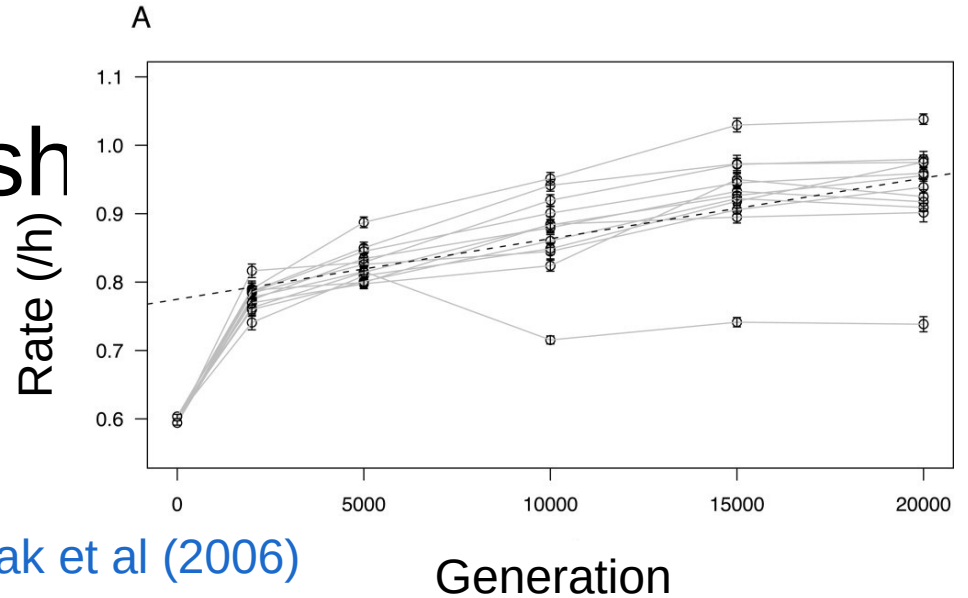
$$\frac{dN}{dt} = r * N * \left(1 - \frac{N}{K}\right)$$



Reminder:  $r$  (growth rate) is *private*,  
 $K$  (yield) is *shared*



What would you expect to happen to *E. coli* during thousands of generations of evolution in well-mixed medium (LTEE)?



# Cooperation and selfishness in the LTEE?

From [Vasi et al \(1994\)](#)

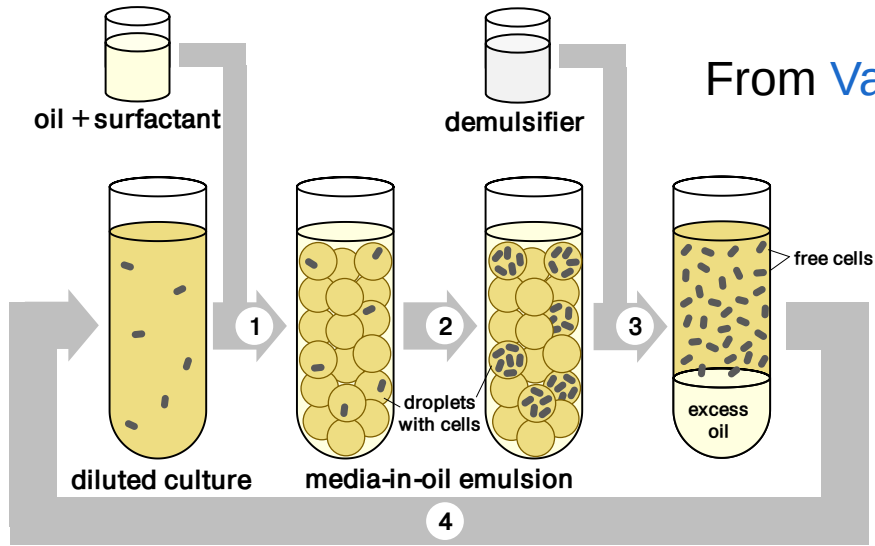
Life-History Trait	Mean for Common Ancestor	Mean for Derived Genotypes
Relative fitness:		
$W$	(1)	1.3486
Fitness components:		
$L$ (h)	1.5264	1.2470
$V_m$ ( $h^{-1}$ )	.7726	.8887
$K_s$ ( $\mu g mL^{-1}$ )	.0727	.0880
$D$ ( $h^{-1}$ )	-.0127	.0029
Other life-history traits:		
$Y$ ( $\times 10^6 \mu g^{-1}$ )	2.6352	1.8386
$D'$ ( $h^{-1}$ )	.0216	.0156
$Z_s$ (fL)	.3546	.6549
$Z_e$ (fL)	.5678	1.1357

But...

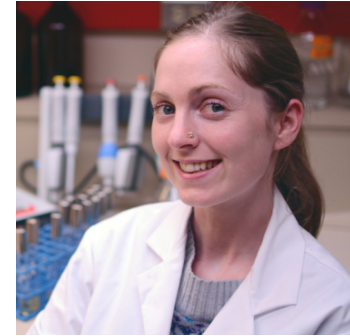
... and *numerical* yield decreased!

... cell size increases ...

# Cooperation and selfishness in the LTEE?



From [Van Raay et al \(2021\)](#)



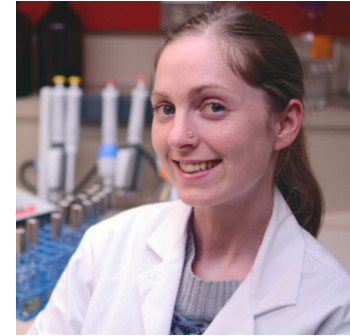
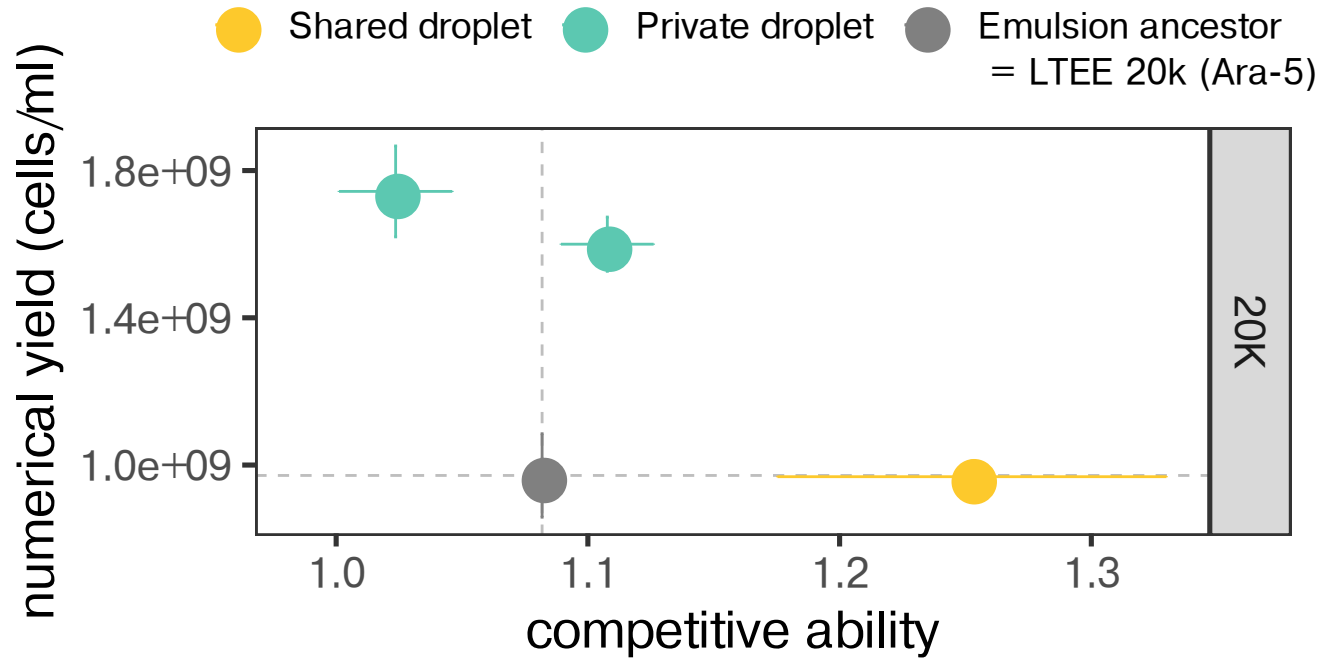
Katrina van Raay

Use of a media-in-oil setup to re-evolve LTEE descendant in more or less structured setting



Luis Zaman

# Cooperation and selfishness in the LTEE?



Katrina van Raay



Luis Zaman

From [Van Raay et al \(2021\)](#)