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# The Generalized Theory of Evolution

## Düsseldorf 2018

### The Evolution of Multicellularity:

# Cheating Done Right

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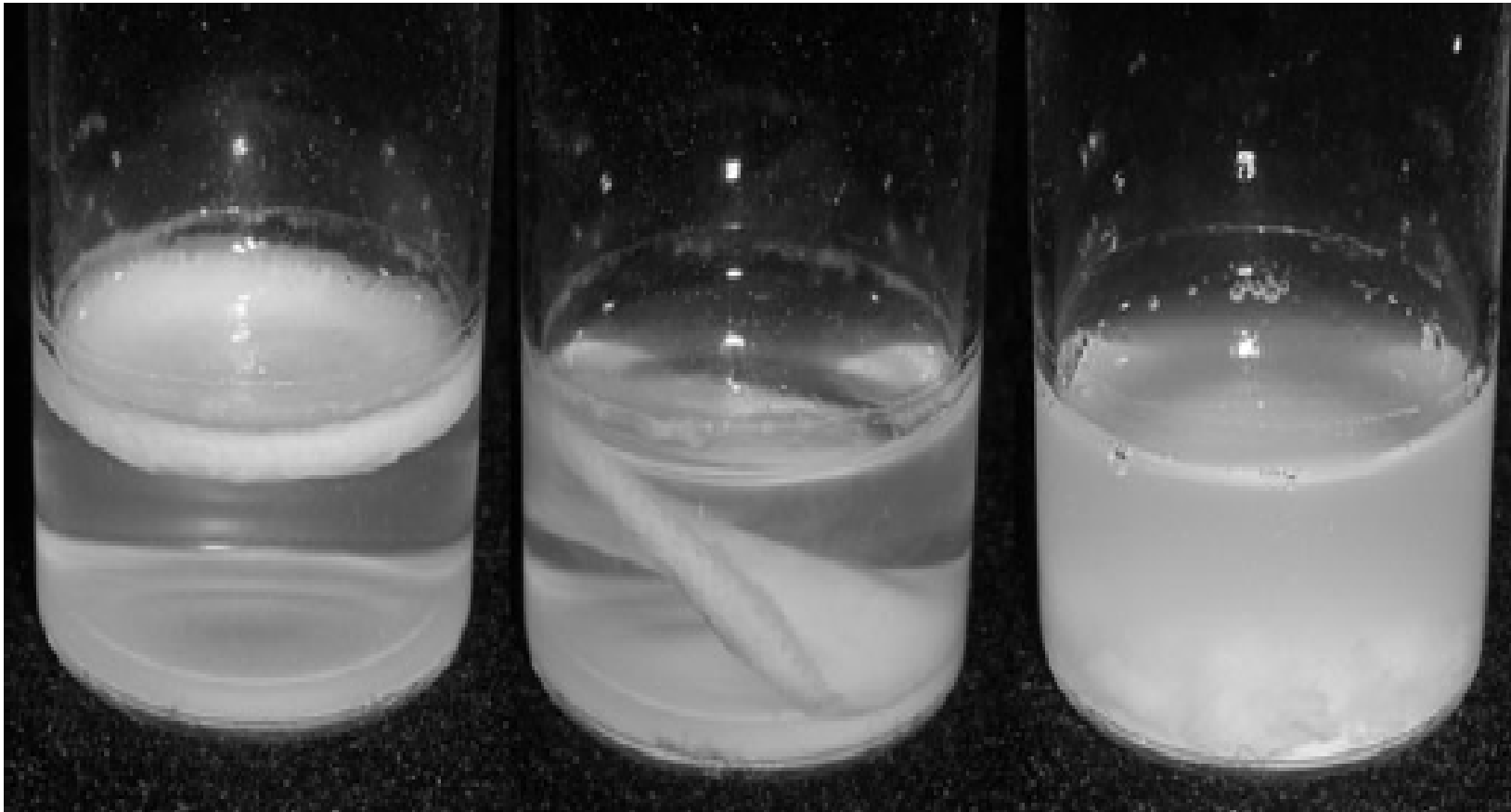
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## 3.0 The Experiment (Hammerschmidt et al.)

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“Life cycles, fitness decoupling and the evolution of multicellularity” (2014)



Rainey (2010, p. 875)

# Outline

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1. The Problem
2. The Solution
3. The Experiment
4. The Verdict
5. The Q&A

# 1.0 The Problem

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*Evolution and the Levels of Selection,*  
Samir Okasha (2006):

*“[M]ulticelled organisms did not come from nowhere, and a complete evolutionary theory must surely try to explain how they evolved, rather than just taking their existence for granted. So levels of selection other than that of the individual organism must have existed in the past, whether or not they still operate today.” (p. 17)*

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# 1.0 The Problem

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**How did the transition(s) from single-cell organisms to multicellular organisms occur?**

**Traditional answer: Cooperation**

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# 1.0 The Problem

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Traditional answer: **Cooperation**

Not sufficient for a transition in  
**Darwinian individuality!**

# 1.0 The Problem

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## **Needed:**

- **Mechanism of group reproduction**
- **Mechanism to minimize the adverse effects of cheats**

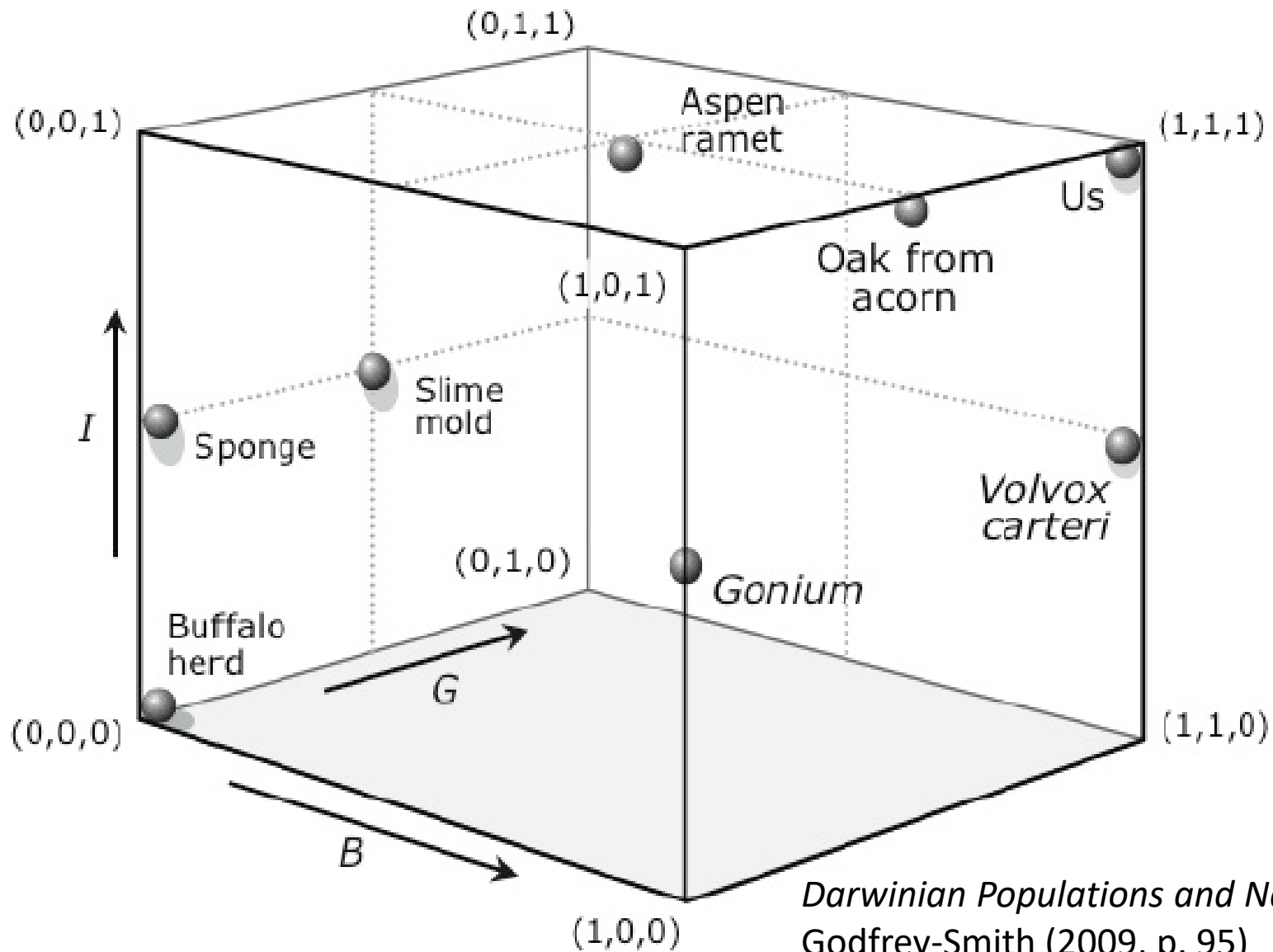
## 2.0 The Solution

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### **The Solution:**

- 1. Multi-level selection (models)**
- 2. Experiments**





*B*: Bottleneck  
*G*: Reproductive specialization (germ/soma)  
*I*: Overall integration

## 2.1 The Solution: Multi-Level Selection

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In multilevel selection [1]:

- (1) "Group selection" refers to the effects of group membership on individual fitness.
- (2) Fitnesses are **properties of individuals**.
- (3) Characters are values attributed to **individuals** (including both individual and contextual characters - see below).
- (4) Populations consist of **individuals, organized into groups**.
- (5) Explicit inferences can be made only about the changing proportions of different kinds of individuals in the whole population (the metapopulation).

"In multilevel selection [2]:

- (1) "Group selection" refers to change in the frequencies of different kinds of groups.
- (2) Fitnesses are **properties of groups**.
- (3) Characters are values attributed to **groups** (including both aggregate and global characters - see below).
- (4) Populations consist of **groups, composed of individuals**.
- (5) Explicit inferences can be made only about the changing proportions of different kinds of groups in the population" (p. 410; **Damuth and Heisler**)

## 2.1 The Solution

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### **Necessary:**

- Mechanism of group reproduction
- Mechanism to minimize the adverse effects of cheats

### **Solution: CHEATS**

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## 2.2 The Solution: Paul Rainey's hypothesis

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### CHEATS:

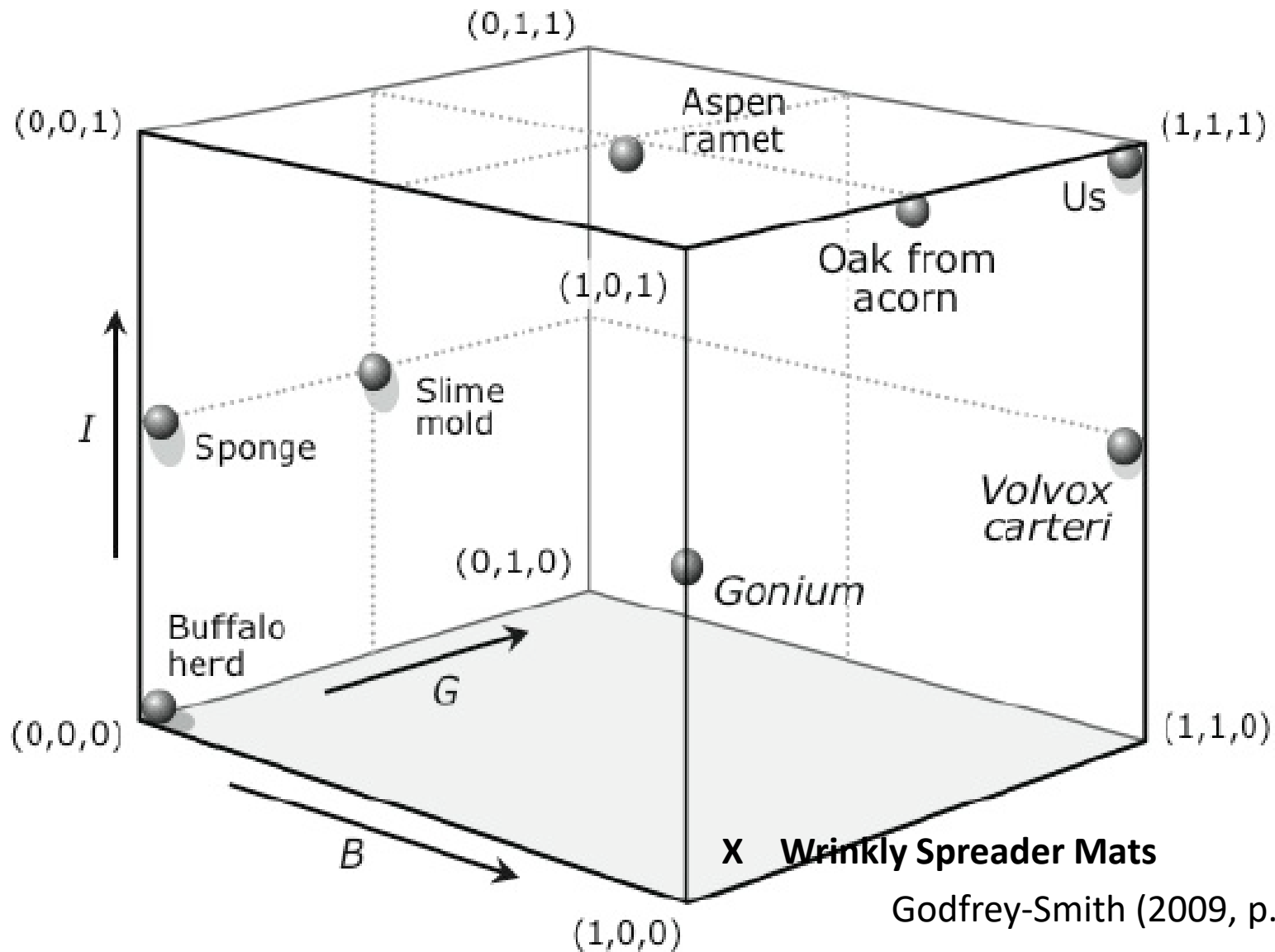
- Proto germ-line propagule detaching itself
- Primitive life cycle switching between WS mats and mutant propagules
- Mutant propagules, once detached, need to switch back to cooperation forming a new individual
  - “Working for the organism”
- Move from MLS1 to MLS2 i.e. **fitness decoupling**

## 2.2 The Solution: Paul Rainey's hypothesis

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Transition towards a **new Darwinian individual**:

- ✓ a **bottleneck** during which a propagule marks the beginning of a new life cycle
- ✓ a germ line being **specialized** for reproduction of the collective
- ✓ **overall integration** of the individuals forming a new individual rather than just a group



Godfrey-Smith (2009, p. 95)

$B$ : Bottleneck

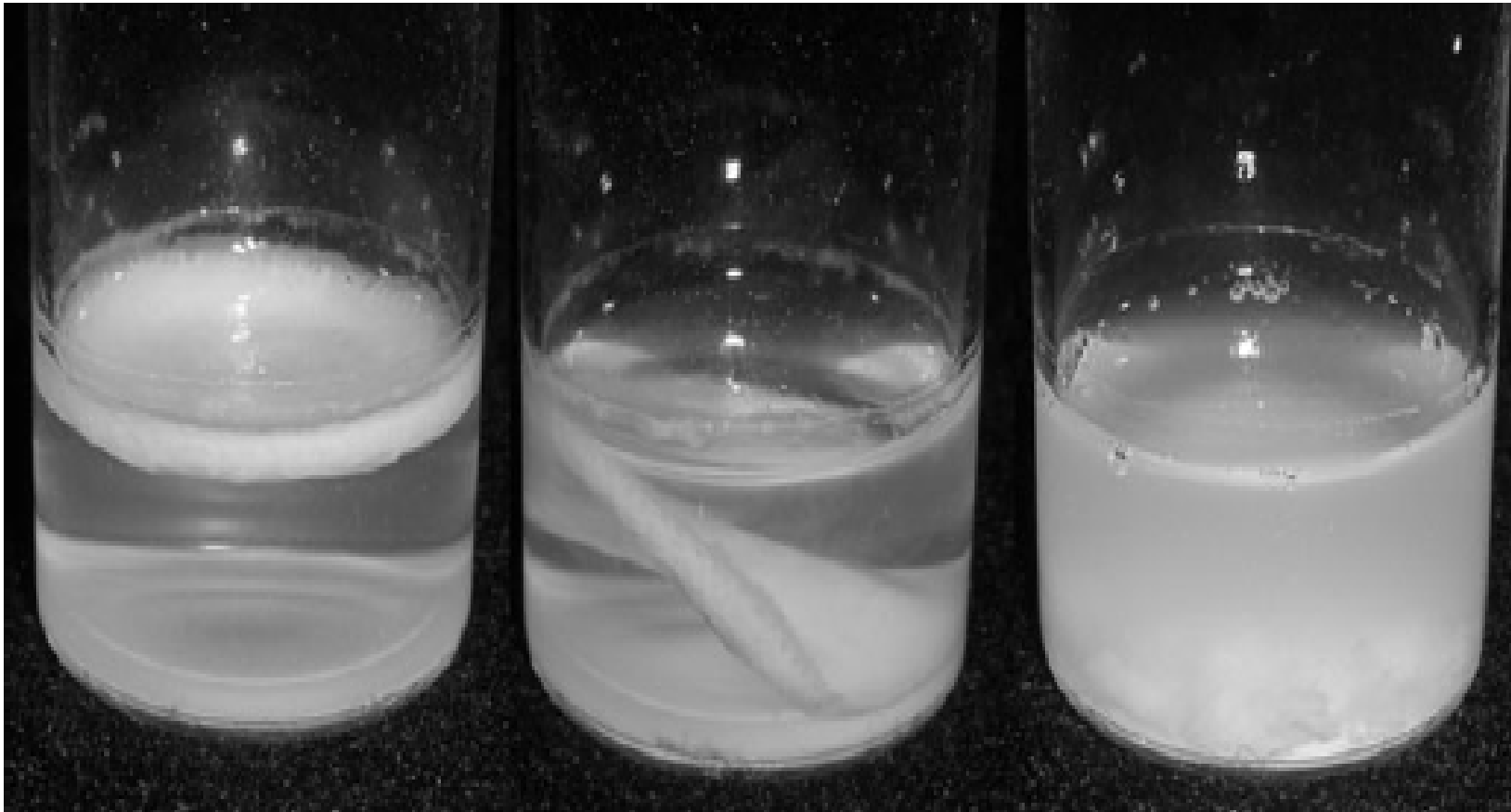
$G$ : Reproductive specialization (germ/soma)

$I$ : Overall integration

## 3.0 The Experiment (Hammerschmidt et al.)

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- Experimental organism: *Pseudomonas fluorescens*



Rainey (2010, p. 875)

## 3.0 The Experiment

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- Spatially structured, undisturbed microcosms
- ancestral 'smooth' genotype (**SM**)
- mutant: 'wrinkly' spreaders (**WS**) produce **costly glue**
  - Survive by **reaping the benefits** of access to oxygen by forming mats, i.e. cooperation (given appropriate ecological conditions)
  - **Tragedy of the commons:** Spread of mutants in the mat leads to the doom of all.



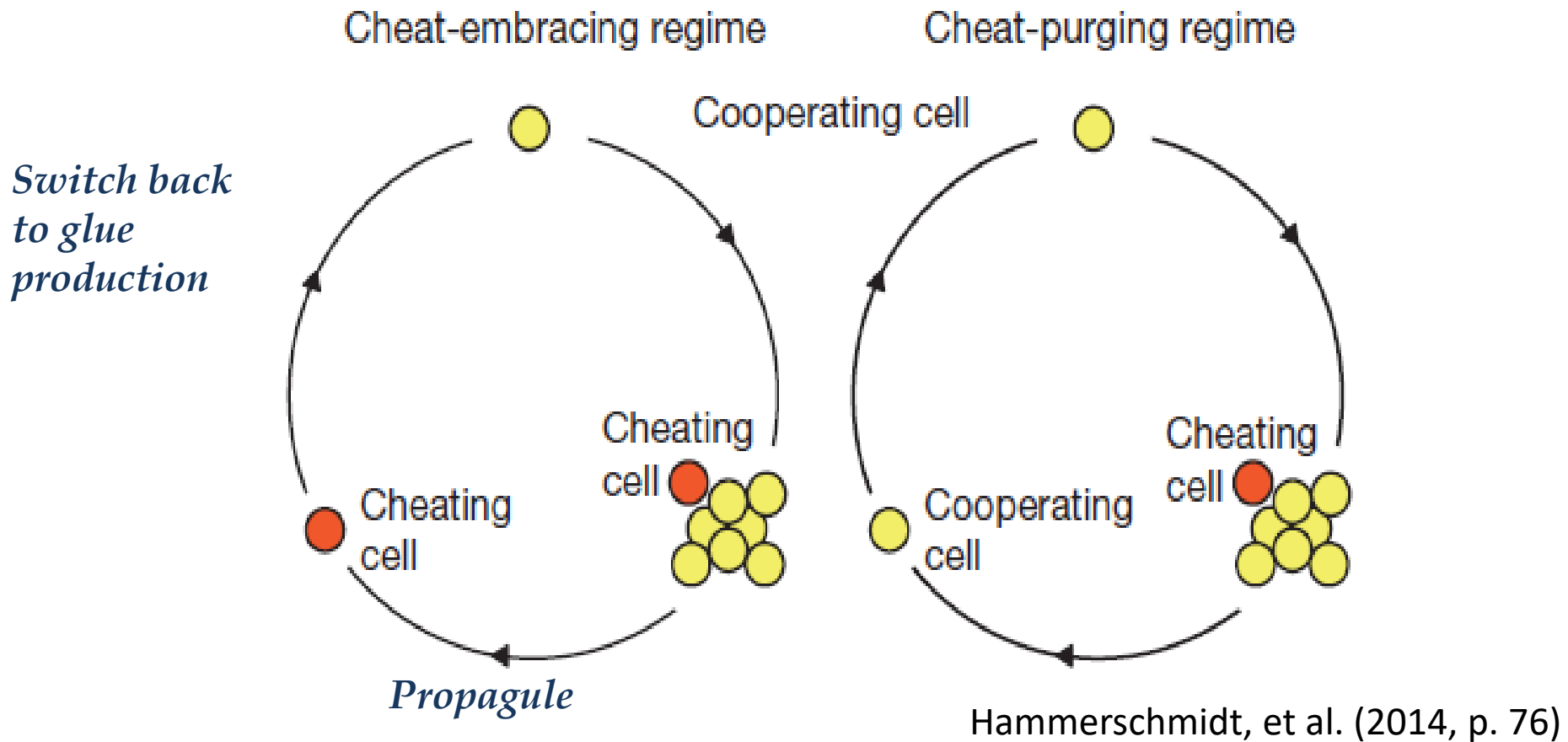
## 3.1 The Experiment: Result

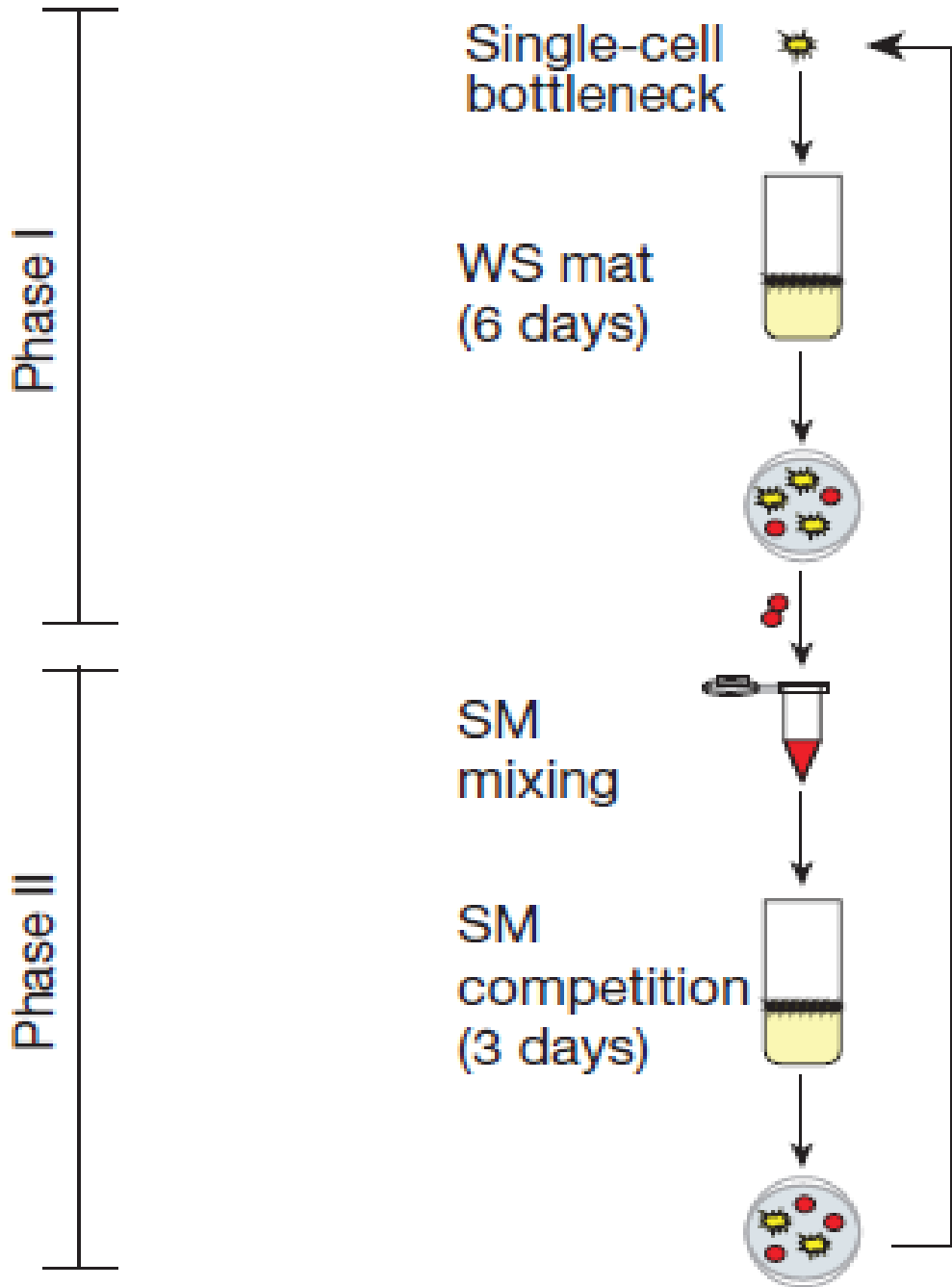
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- Conflict between “cooperating” WS cells and cheats (SM) gives evolution something to act on
- WS mats are like soma an **evolutionary dead-end**
- Fitness of mats becomes **decoupled** in cheat-embracing regime, **NOT** in the cheat-purging regime

## 3.2 The Experiment (Hammerschmidt et al.)

- Two regimes:





Causes of extinction:

No WS mat  
  
*Failure to develop*

No SM  
  
*Failure to create a propagule*

No WS  
  
*Failure to develop*

## 4.0 The Verdict

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*Evolution and the Levels of Selection,*

Okasha (2006):

*“The study of evolutionary transitions is still in its infancy, with much empirical work remaining to be done, so it is difficult to say whether the foregoing analysis will prove satisfactory in all respects. But whatever future developments in the field look like, it is likely that multi-level selection will remain crucial for theorizing about evolutionary transitions” (p. 240).*

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## 4.0 The Verdict

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- Cheat-embracing regime decouples the fitness of the mat from the fitness of the cells
    - The mats with the highest fitness consist of cells with lower individual fitness
    - Cells start to “work” for the mat-organism
  - Hypothesis: **cheats and conflict drive the evolution of multicellularity**
  - Problem of cooperation, group reproduction and minimization of adverse cheats can be solved, **by cheats as the first single-cell propagules** marking the beginning of a **new life cycle through a bottleneck**
    - Introduces **germ/soma distinction** with cheats coming (marginally) under **developmental control**
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# Q&A



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**Thanks!**

