Conceptual perspectives on the problem of cooperation

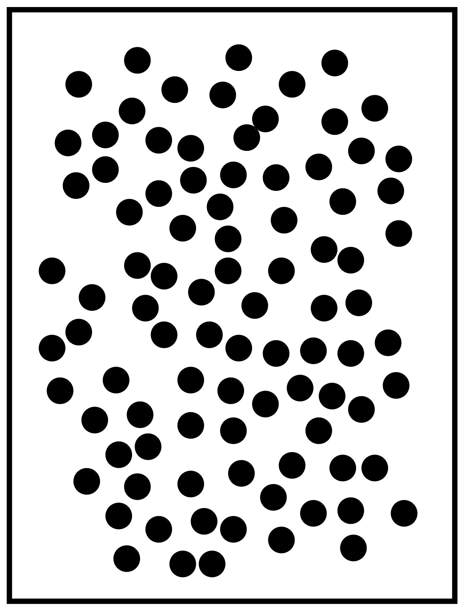
Michael Doebeli, University of British Columbia

KITP, January 2013

Joint work with Jeff Fletcher (Portland State) and Burt Simon (UC Denver)

1. Single-level selection models

2. Multi-level selection models



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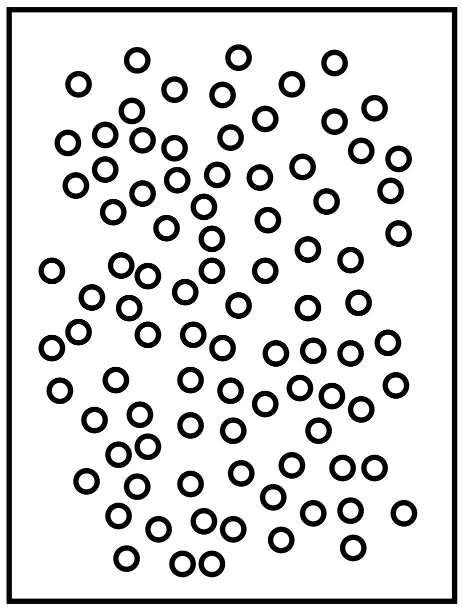

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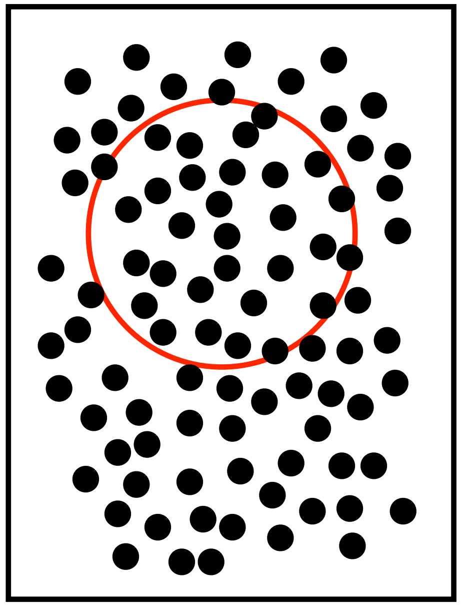

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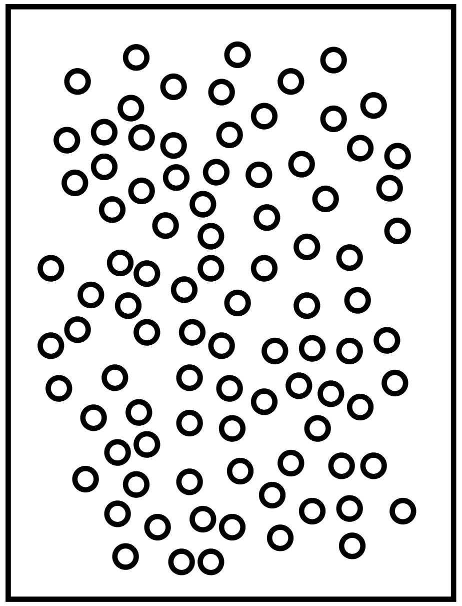

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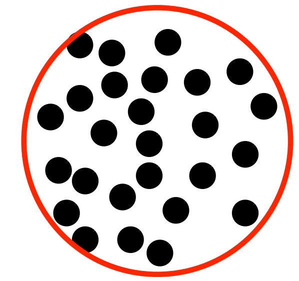

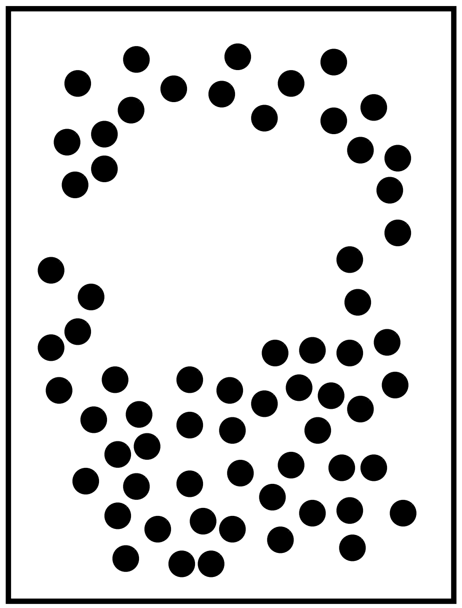

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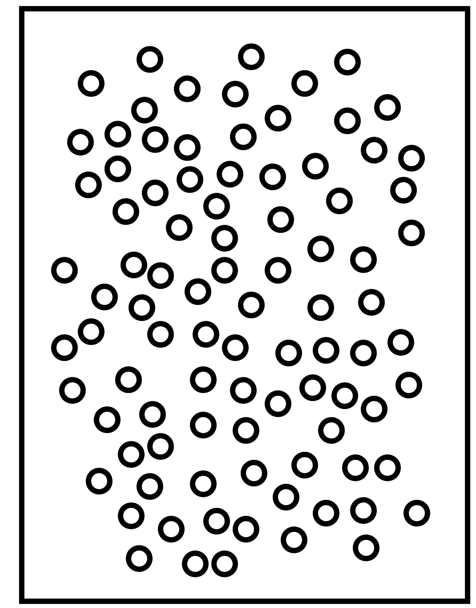

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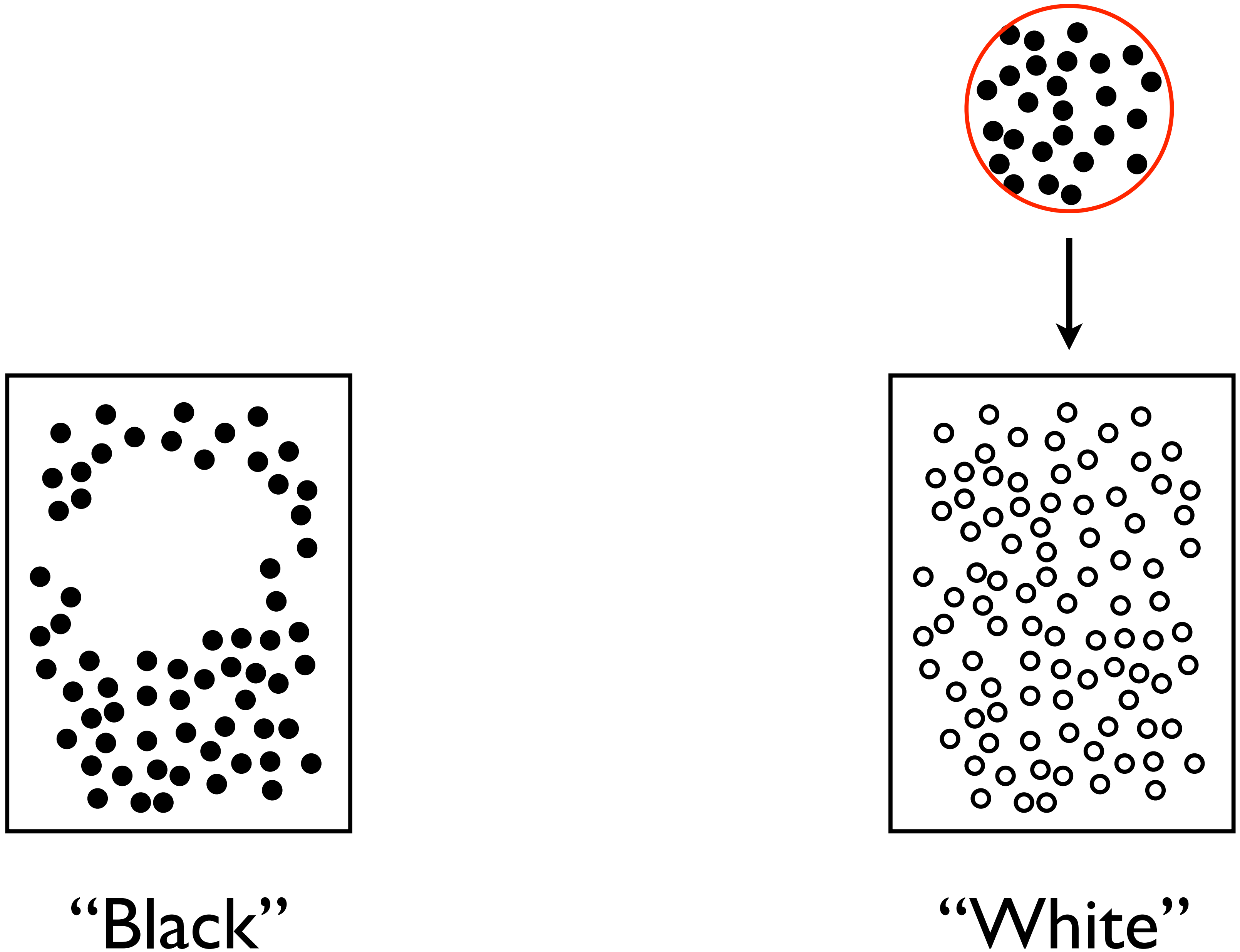
“Black”
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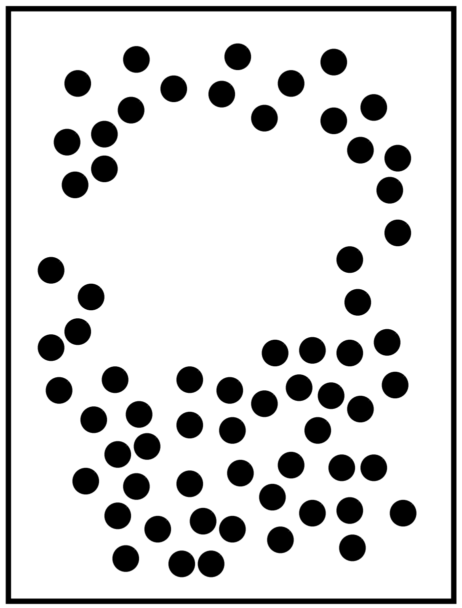

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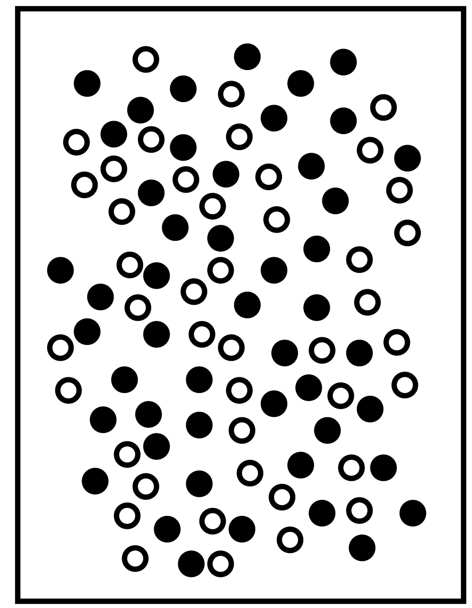

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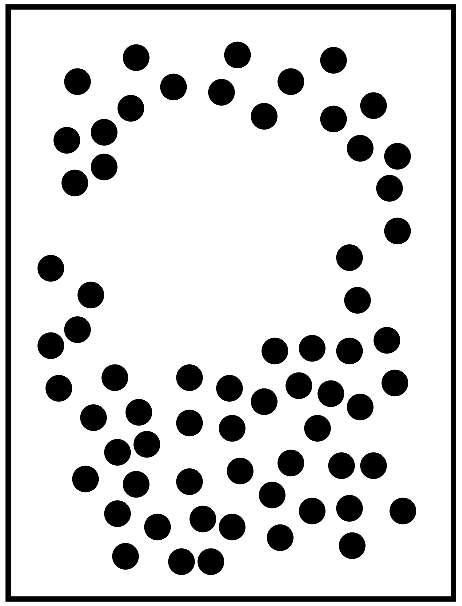

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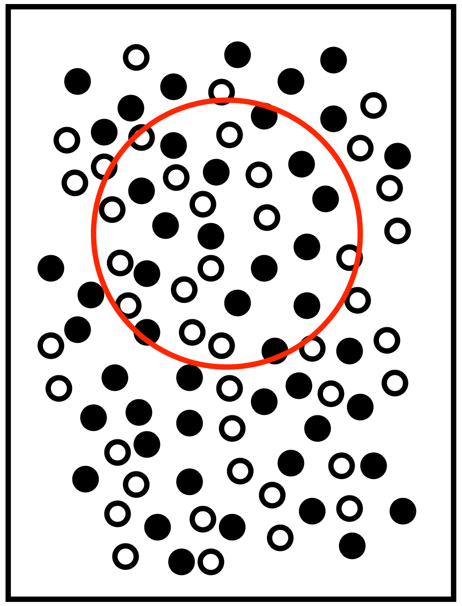

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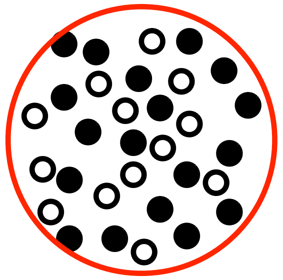

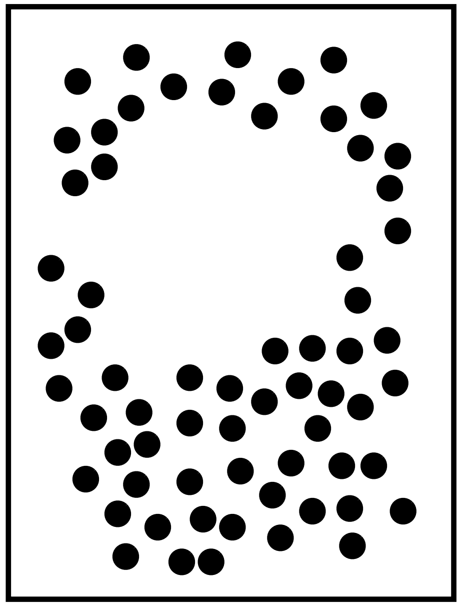

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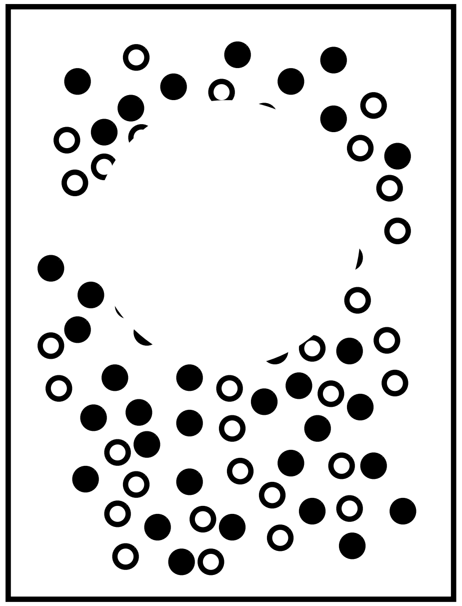

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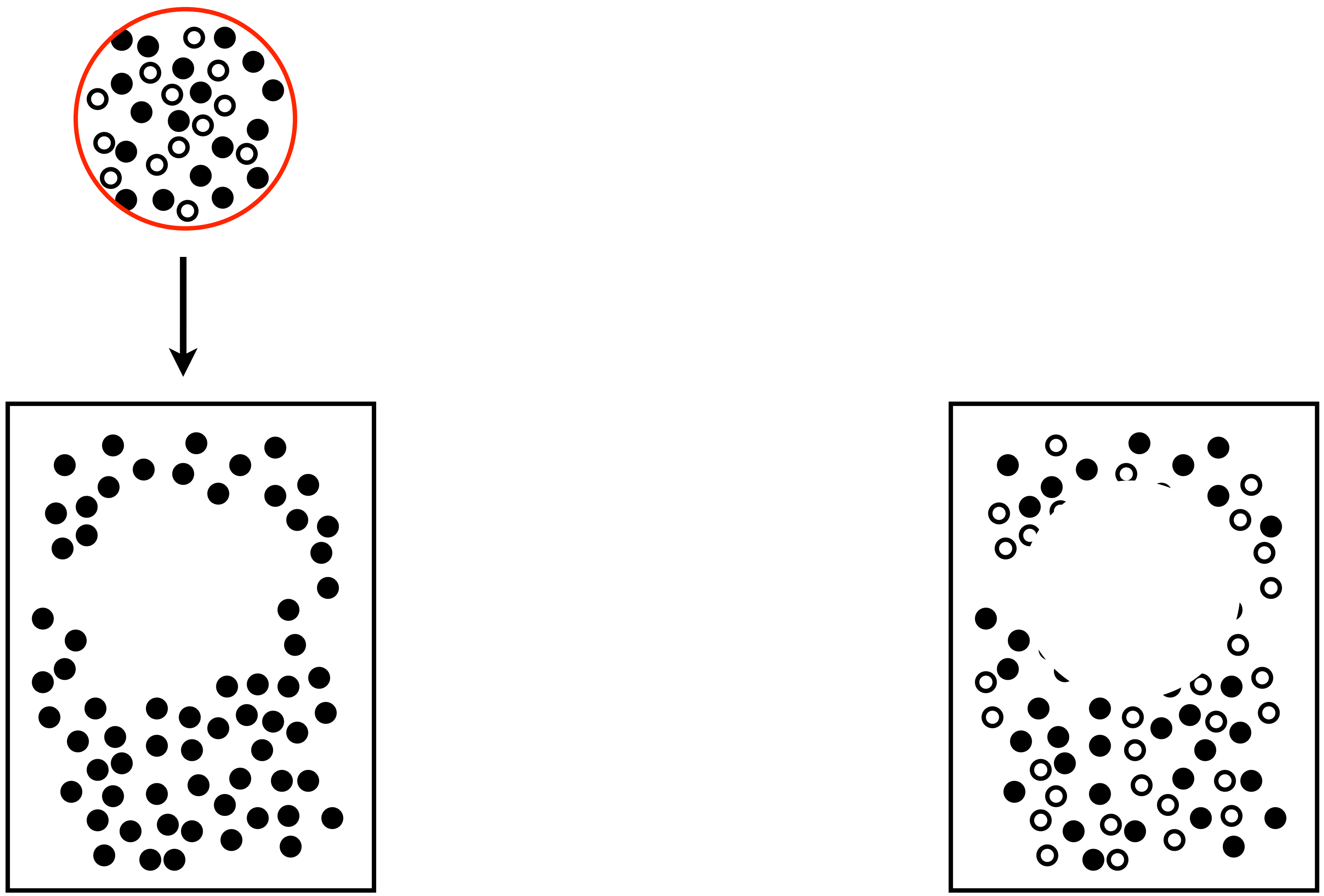
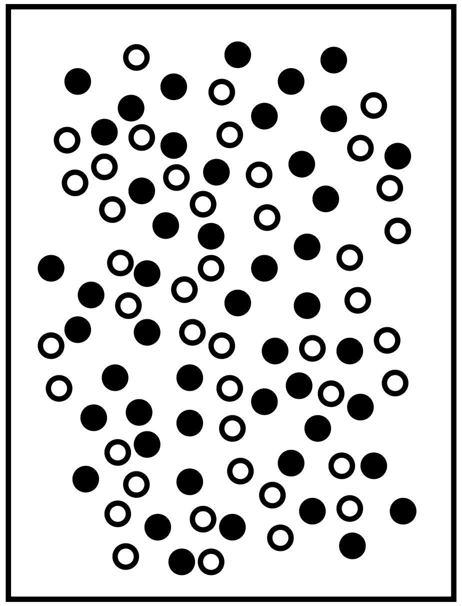


“Black” “White”



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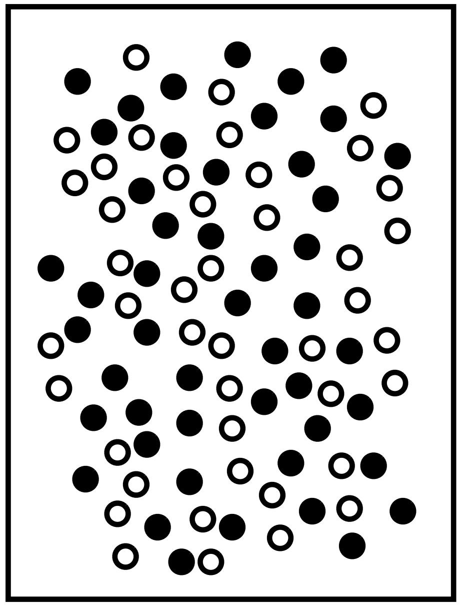
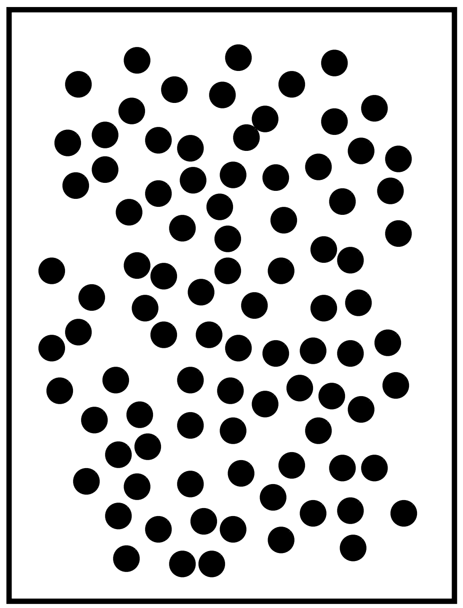


“White”

More black balls in “White” jar than white balls in “Black” jar?
Or vice versa?

1000 black balls



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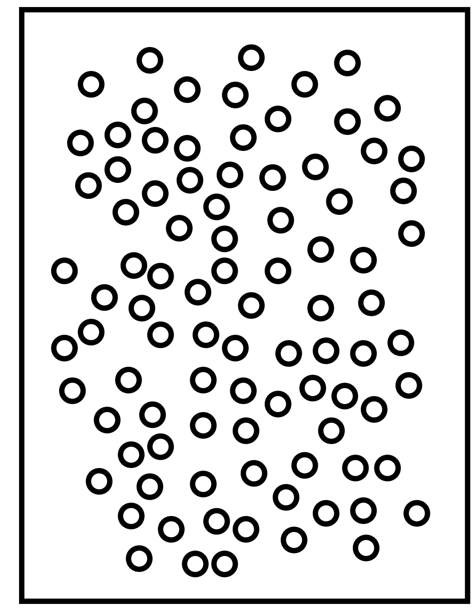
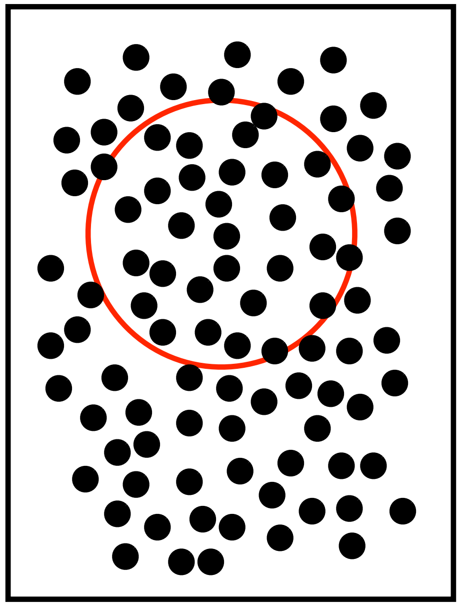


1000 white balls

“White”

1000 black balls



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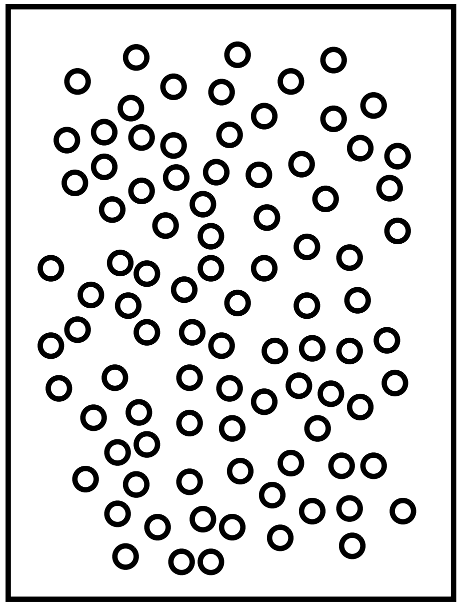

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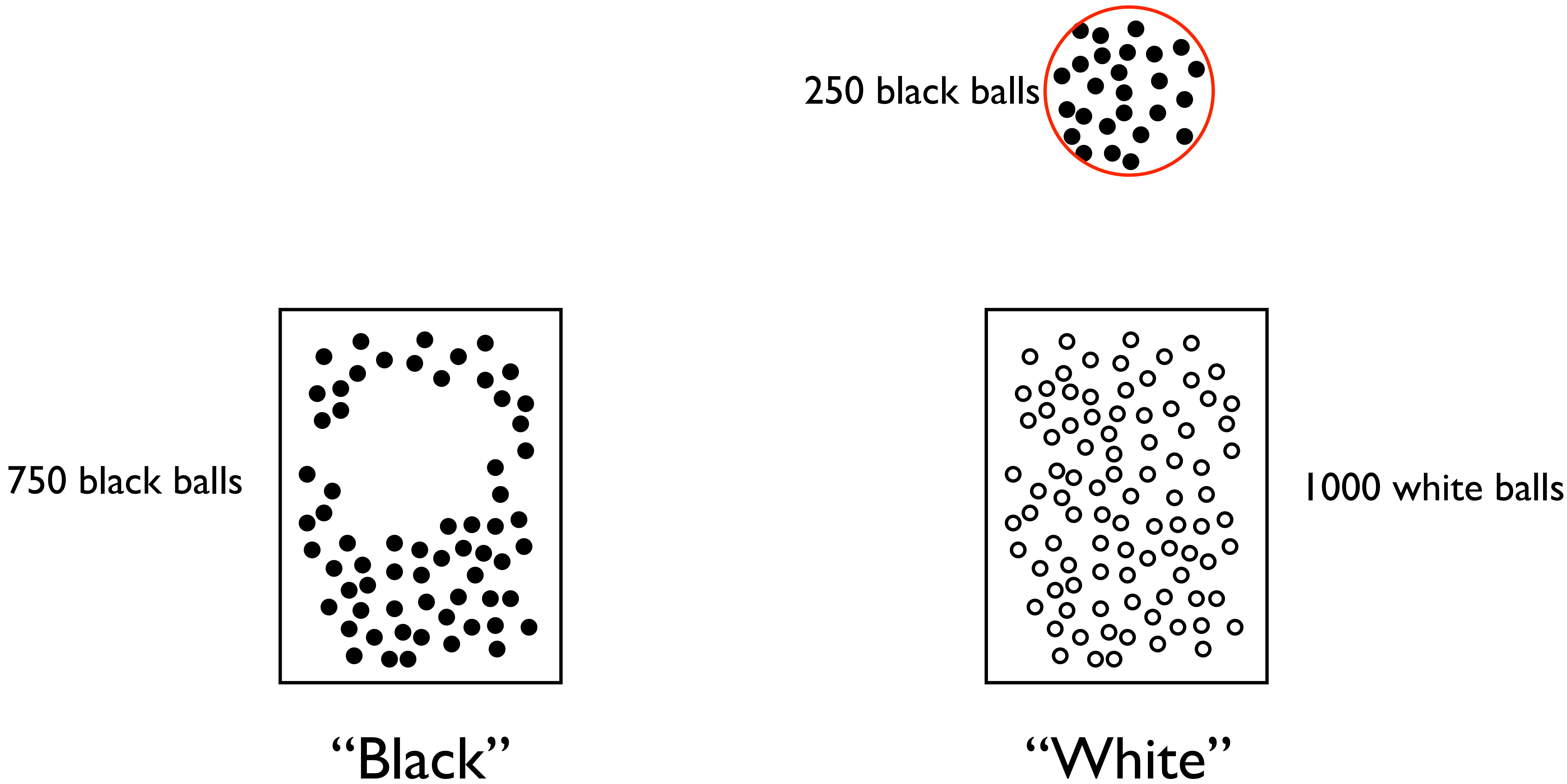
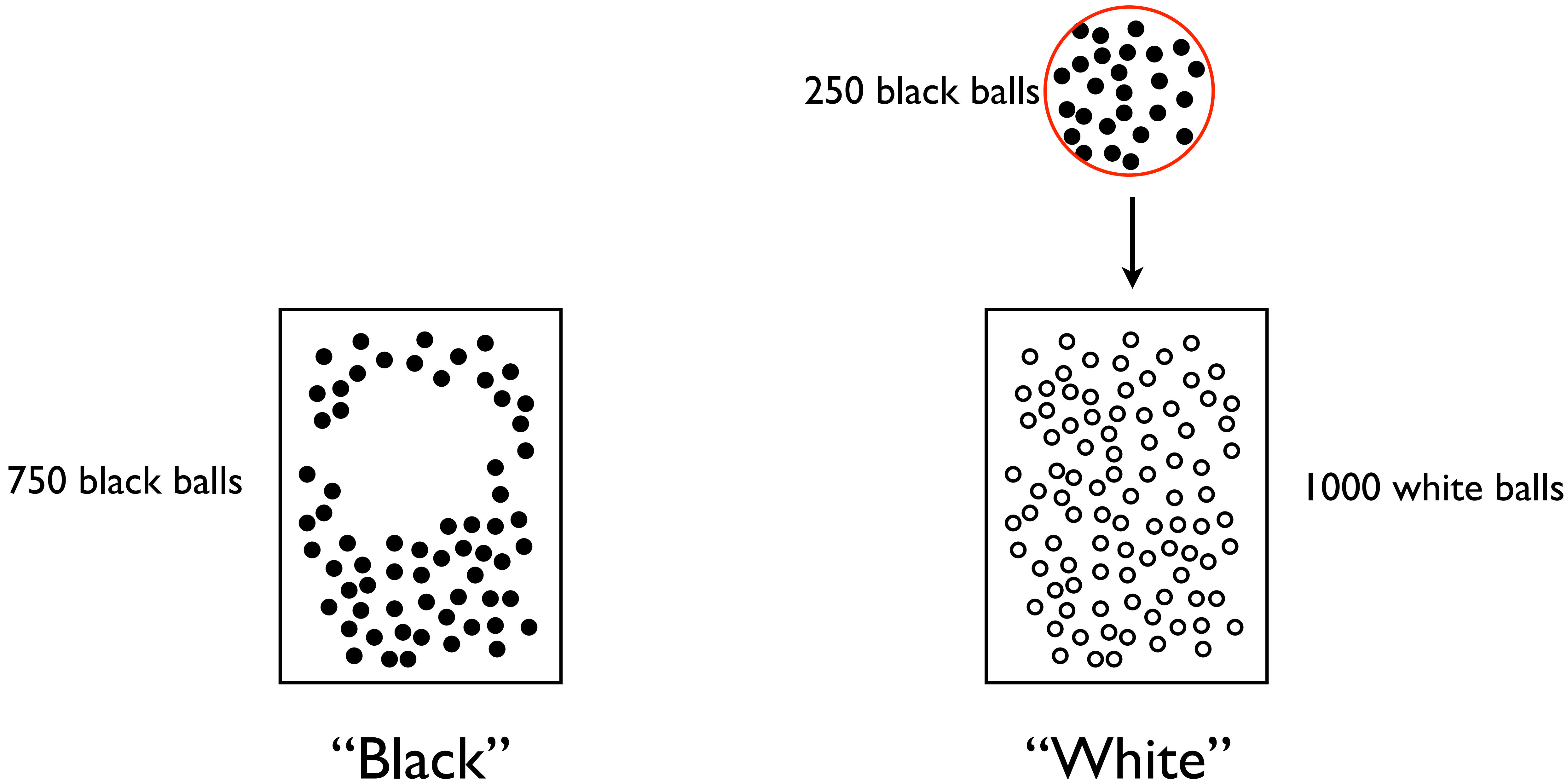

250 black balls
750 black balls
1000 white balls
“Black”
“White”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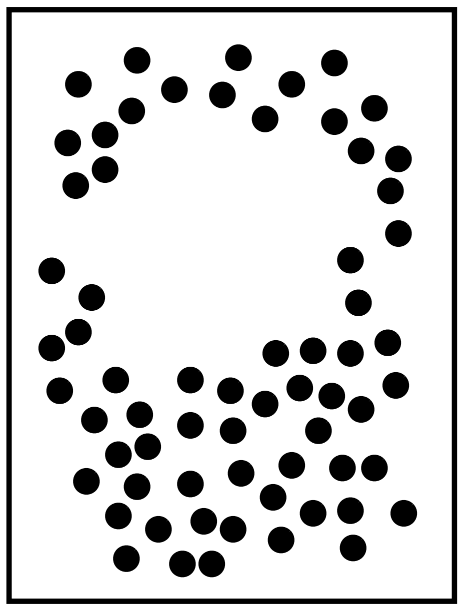
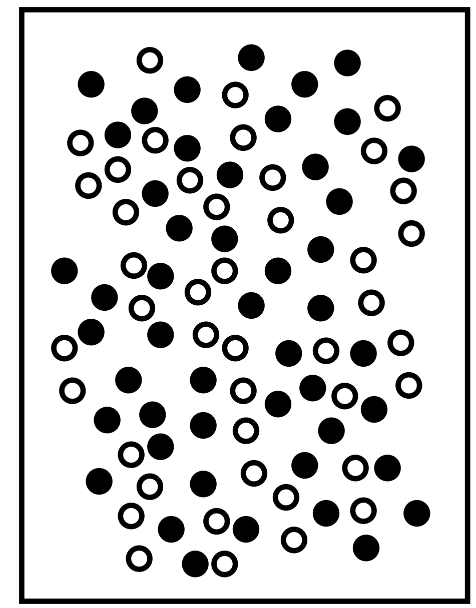
750 black balls



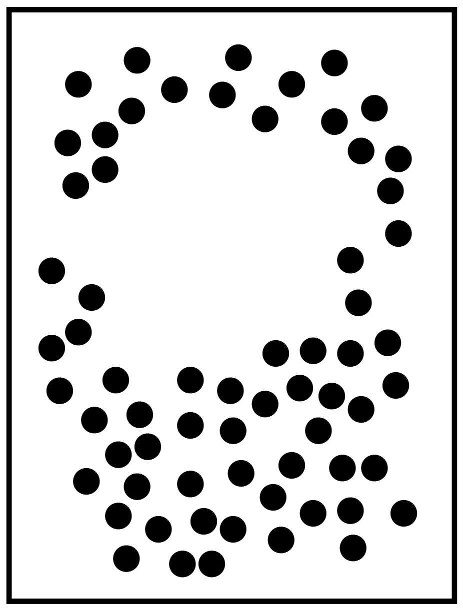
“Black”

1000 white balls,
250 black balls

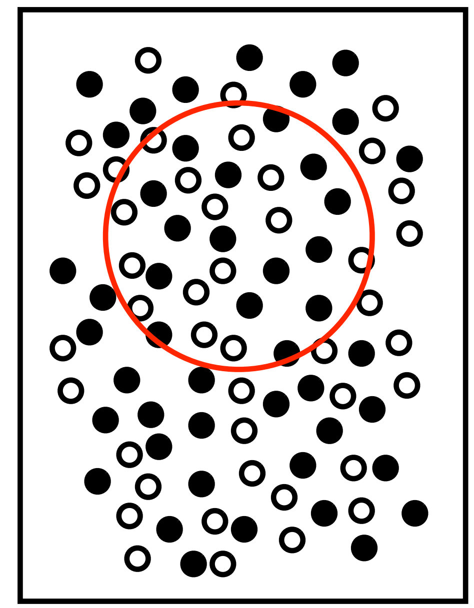


“White”

750 black balls

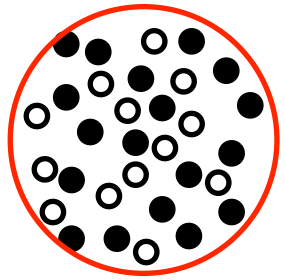


“Black”



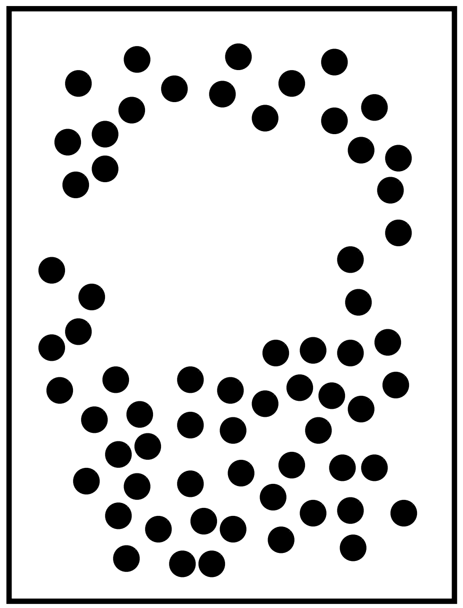
1000 white balls,
250 black balls

“White”



250 balls, say:
193 white balls
57 black balls

750 black balls



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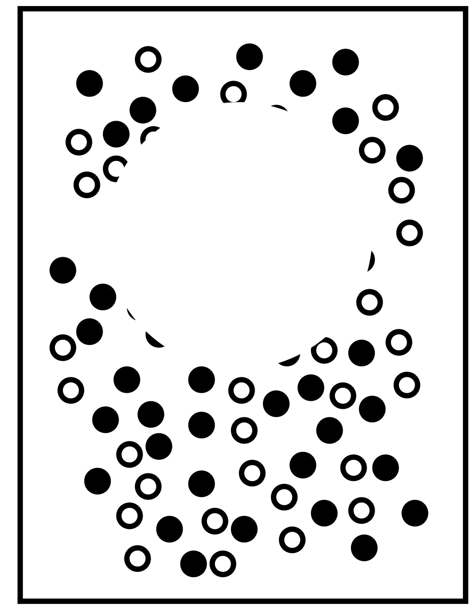

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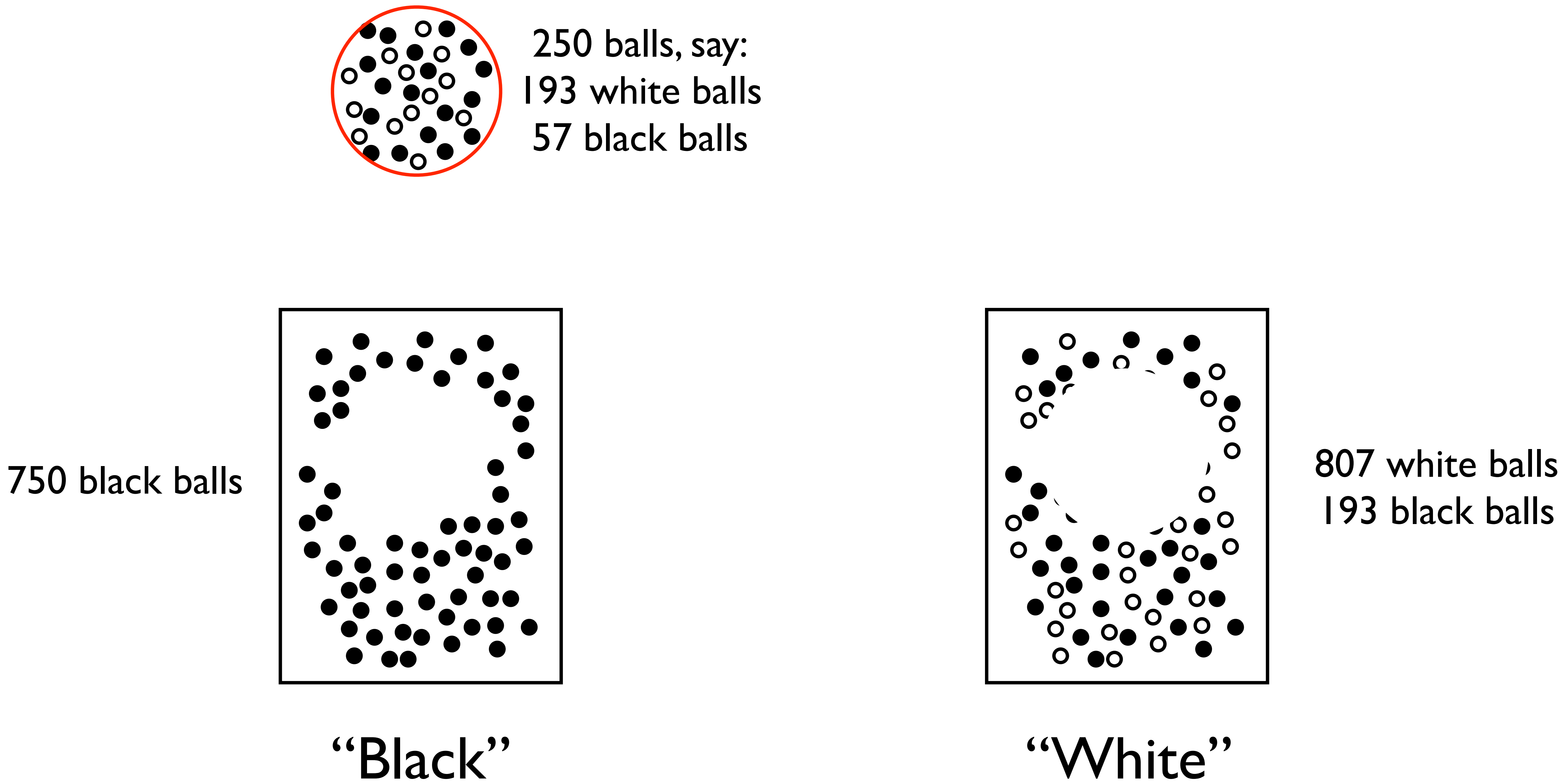
“White”


250 balls, say:
193 white balls
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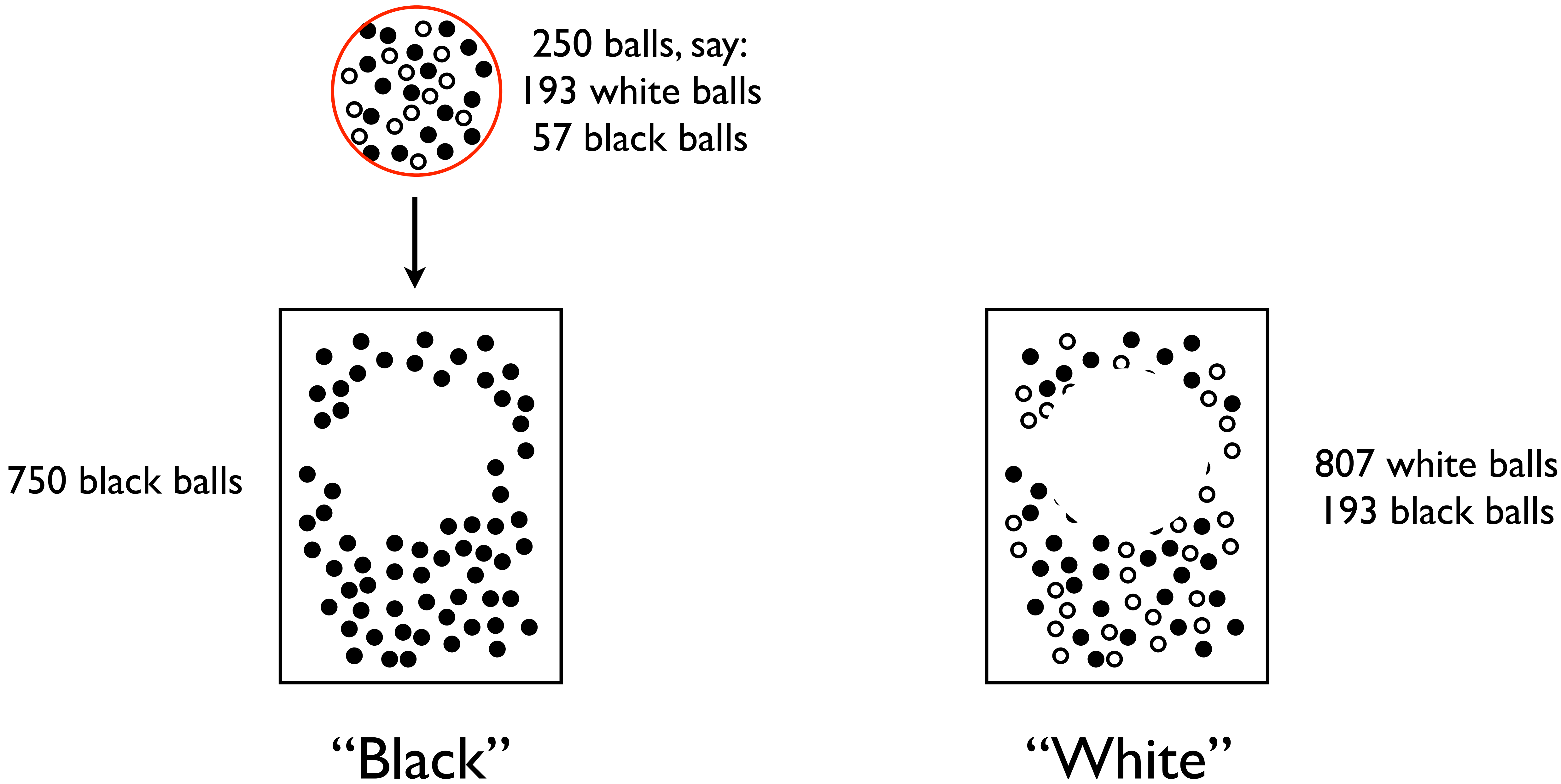
750 black balls
807 white balls
193 black balls
"Black"
"White"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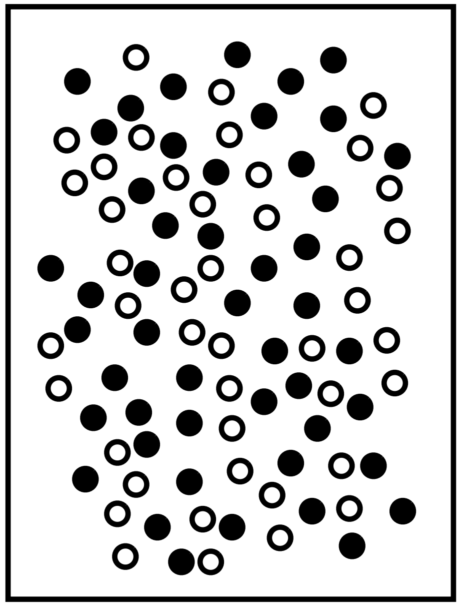

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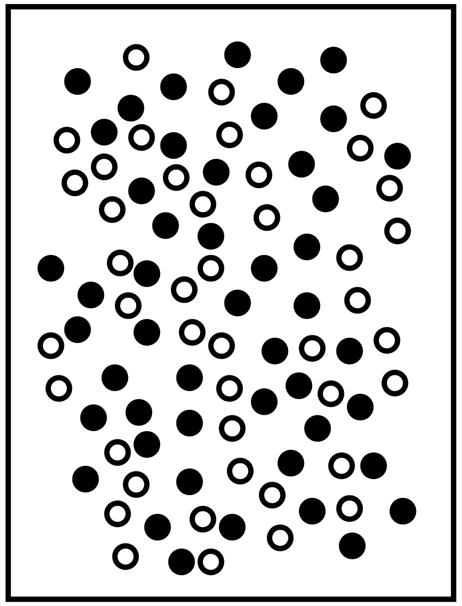

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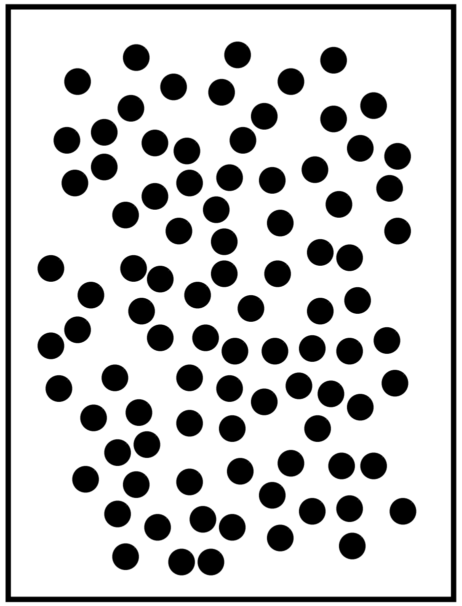

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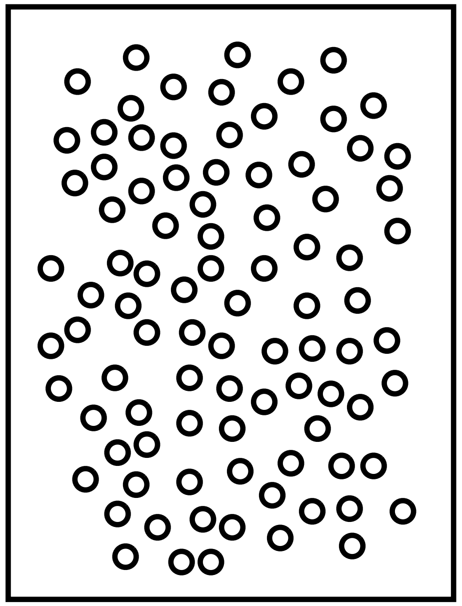

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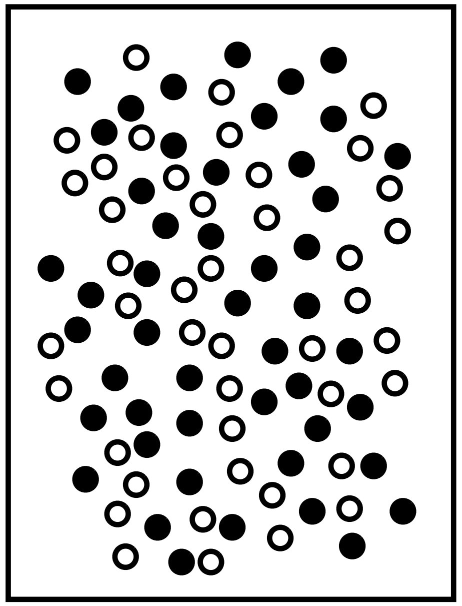

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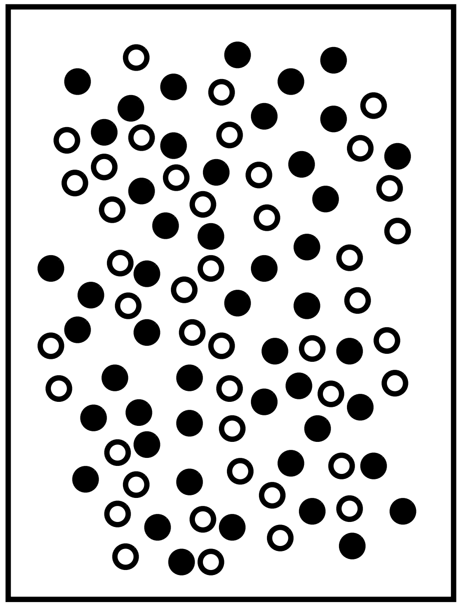

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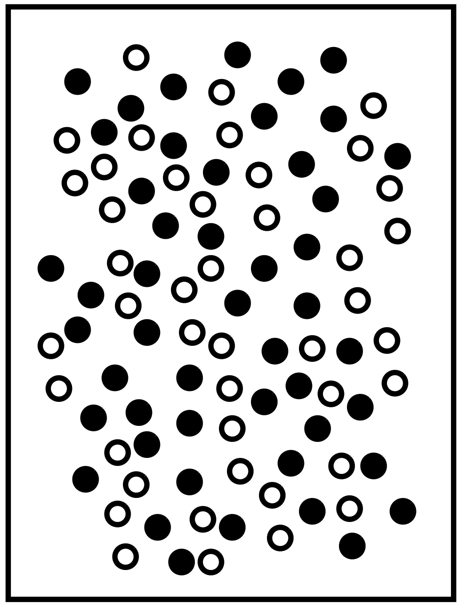

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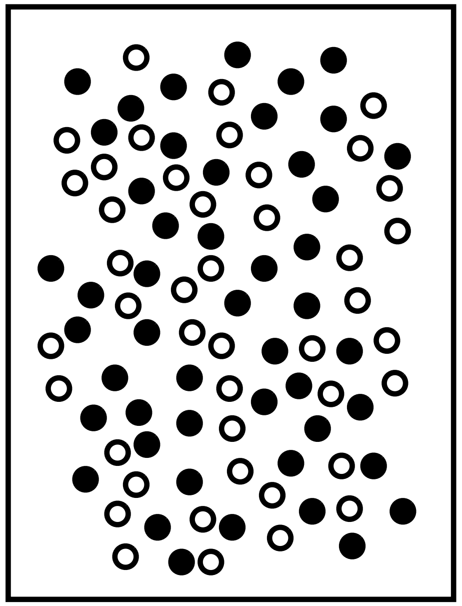

"White"

Easy explanation:
After exchange, same amount of balls in both jars

Public Goods Game (the mother of all cooperation models)

- *C* (Cooperator): contributes *b* to public good at cost *c* ($b > c > 0$)
- *D* (Defector): contributes 0 at no cost
- Interaction group with *N* individuals: *k* Cooperators, *N-k* Defectors
- $k \cdot b$ = public good produced; distributed equally among all group members, each gets $(k \cdot b)/N$

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Payoff structure *within a given interaction group*:

Strategy	Payoff from "self"	Payoff from "interaction environment"	Total payoff
C			
D			

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D			

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D	0	kb/N	kb/N

Within any given interaction group, *C* always does worse than (even with "weak altruism", $b/N - c > 0$)

Population-wide payoffs: average payoff from many different interaction groups

- e_C = # cooperators among N-1 other members of an average interaction group of focal C
  (average interaction environment of a focal C)
- e_D = # cooperators among N-1 other members of an average interaction group of focal D
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C	$b/N - c$		
D			

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D			

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Strategy	Payoff from self	Payoff from average interaction environment	Total payoff
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D			

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Strategy	Payoff from self	Payoff from average interaction environment	Total payoff
C	$b/N - c$	$e_C b/N$	$(e_C + 1)b/N - c$
D	0	$e_D b/N$	$e_D b/N$

C wins if: $e_C + (1 - \frac{cN}{b}) > e_D$

e_C = # cooperators among *N*-1 other members of an average interaction group of focal C

e_D = # cooperators among *N*-1 other members of an average interaction group of focal D

condition for the evolution of cooperation:

$$e_C + (1 - \frac{cN}{b}) > e_D$$

Strong altruism ($b/N - c < 0$) requires $e_C > e_D$

Cooperators must have a more cooperative interaction environment than defectors: **assortment** among cooperators

Example:

Random interactions (random formation of interaction groups):

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C wins if and only if $b/N - c > 0$ (“weak altruism”)

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Evolution of cooperation requires: $$e_C + (1 - \frac{cN}{b}) > e_D = e_C$$

C wins if and only if $b/N - c > 0$ (“weak altruism”)

Note: weak altruism is not enough in general if there is negative assortment ($e_C < e_D$)

Chuang et al, "Simpson's Paradox in a Synthetic Microbial System" Science, 2009

Two E. coli strains:

- strain A secretes inducer of antibiotic resistance (at a cost); inducer = public good
- strain B doesn't produce inducer

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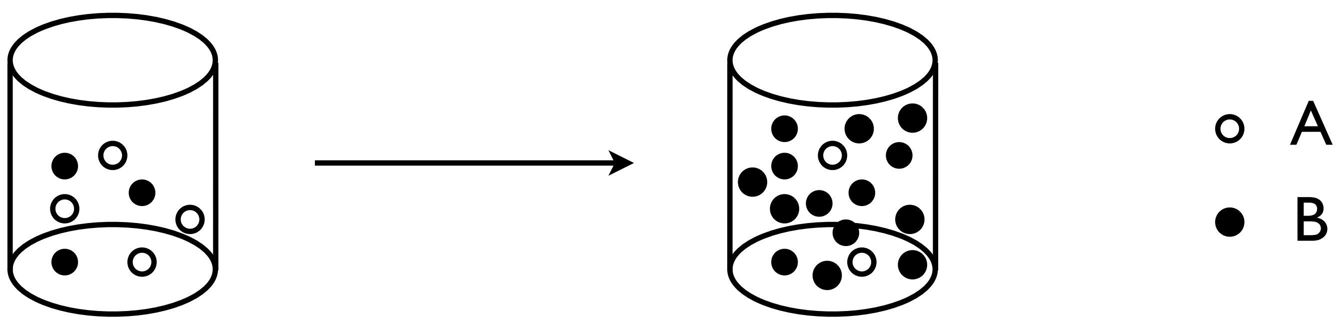
Public goods game:

when growing together in media containing antibiotics, strain B outcompetes strain A



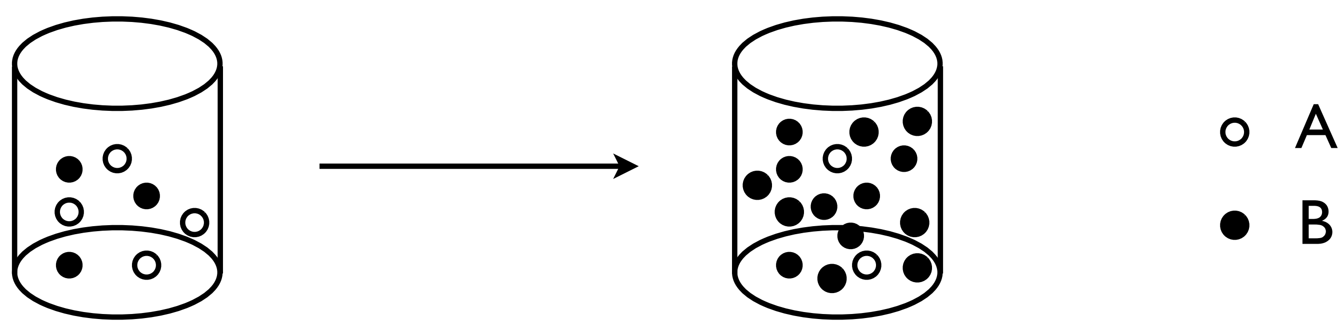
Chuang et al, "Simpson's Paradox in a Synthetic Microbial System" Science, 2009

Two E. coli strains:

- strain A secretes inducer of antibiotic resistance (at a cost); inducer = public good
- strain B doesn't produce inducer

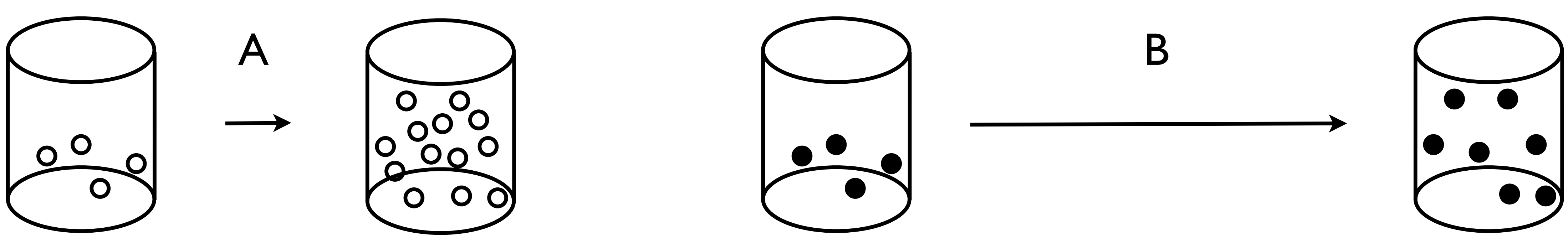
Public goods game:

when growing together in media containing antibiotics, strain B outcompetes strain A



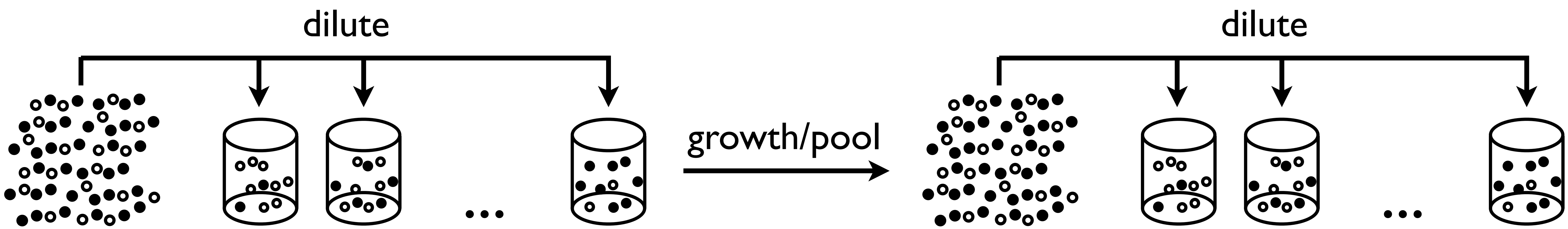
Weak altruism:

when growing in isolation from small initial densities, strain A grows faster than strain B



Experimental evolution:

- common pool of A and B strongly diluted and distributed in many different wells
- growth, then pooling of all well populations, etc



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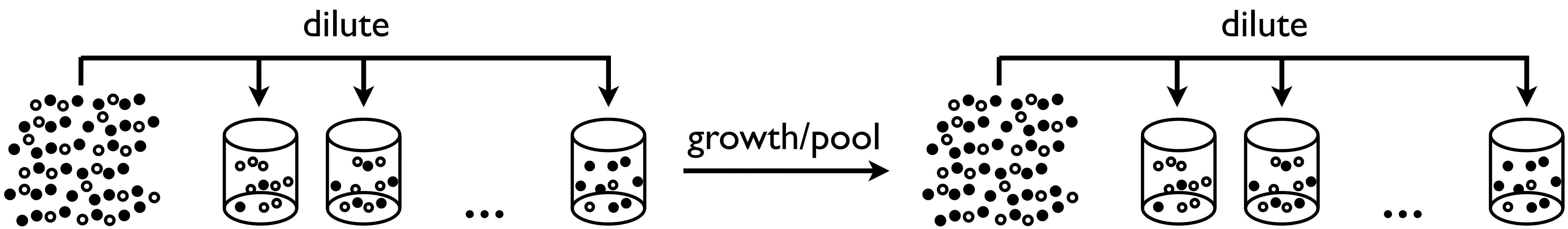
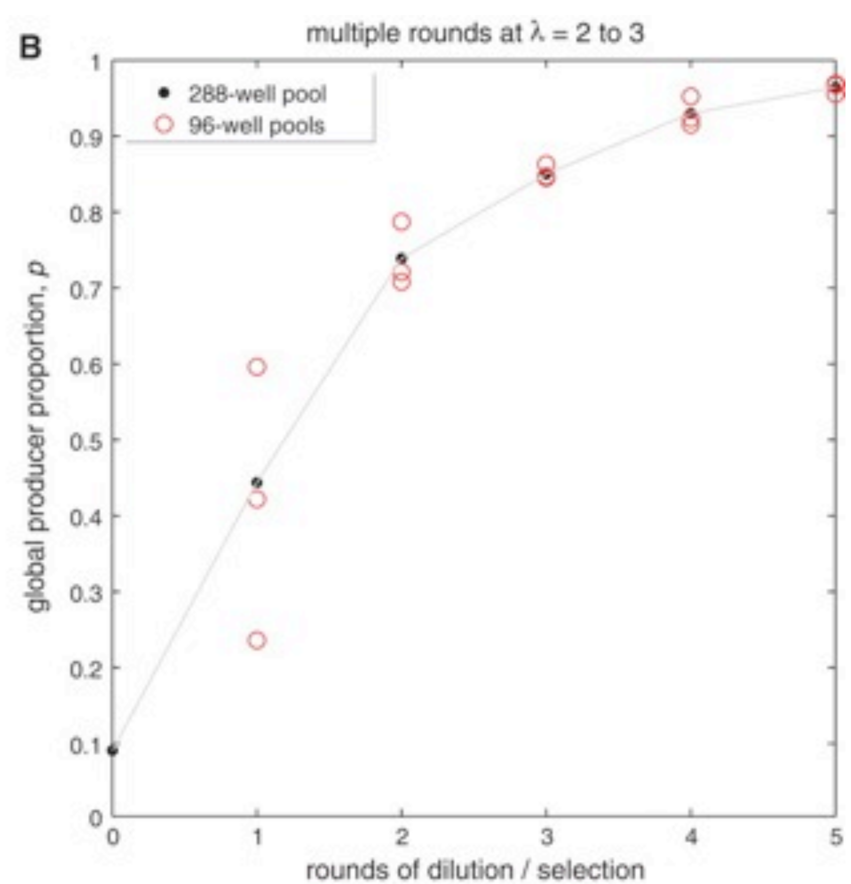
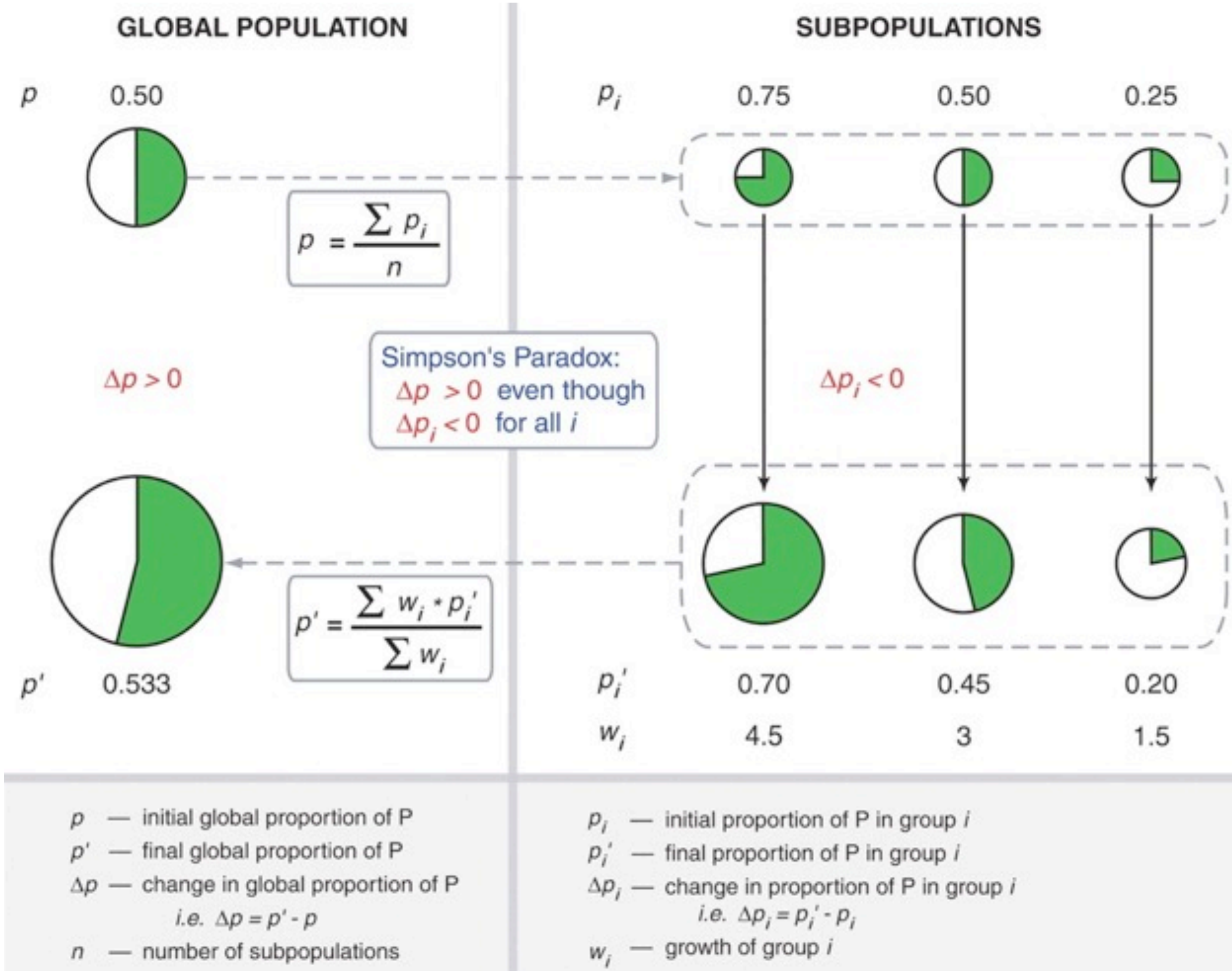


Result: evolution of cooperation (producers increase in pooled frequency)



from Chuang et al, Science, 2009

“Complicated” explanation: Simpson’s paradox



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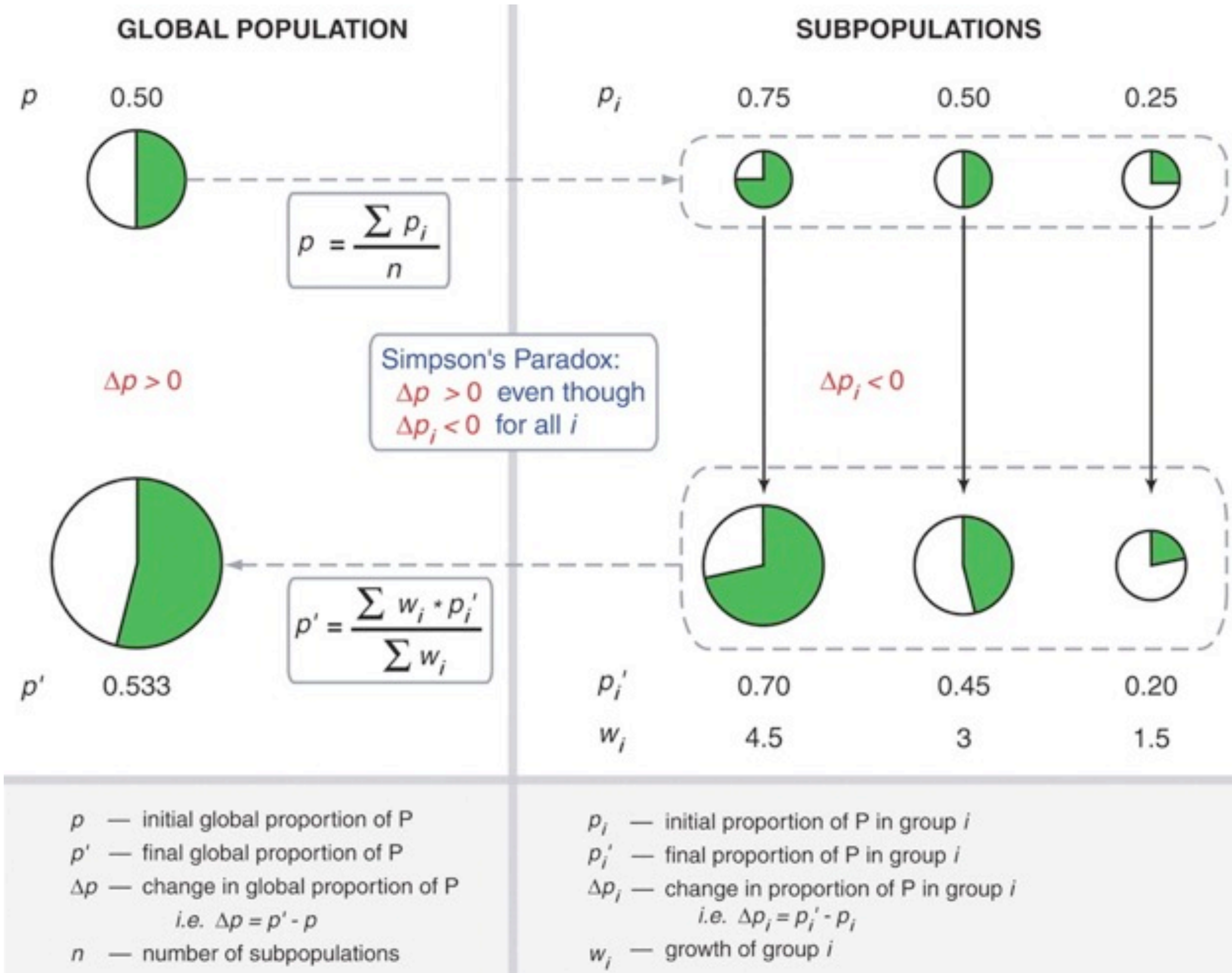

from Chuang et al, Science, 2009

Easy explanation: random interaction groups, weak altruism

e_C = # cooperators among *N*-1 other members of an average interaction group of focal C

e_D = # cooperators among *N*-1 other members of an average interaction group of focal D

condition for the evolution of cooperation: $$e_C + (1 - \frac{cN}{b}) > e_D$$

Examples related to "group selection":

1. Every interaction group contains exactly *k* cooperators (no variation between groups):

   $e_C = k - 1$

   $e_D = k$

   C never wins…

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Examples related to "group selection":

1. Every interaction group contains exactly k cooperators (no variation between groups):

   $e_C = k - 1$

   $e_D = k$

   C never wins…

2. Only two types of interaction groups: all cooperators, or all defectors (maximal group variation):

   $e_C = N - 1$

   $e_D = 0$

   C always wins…

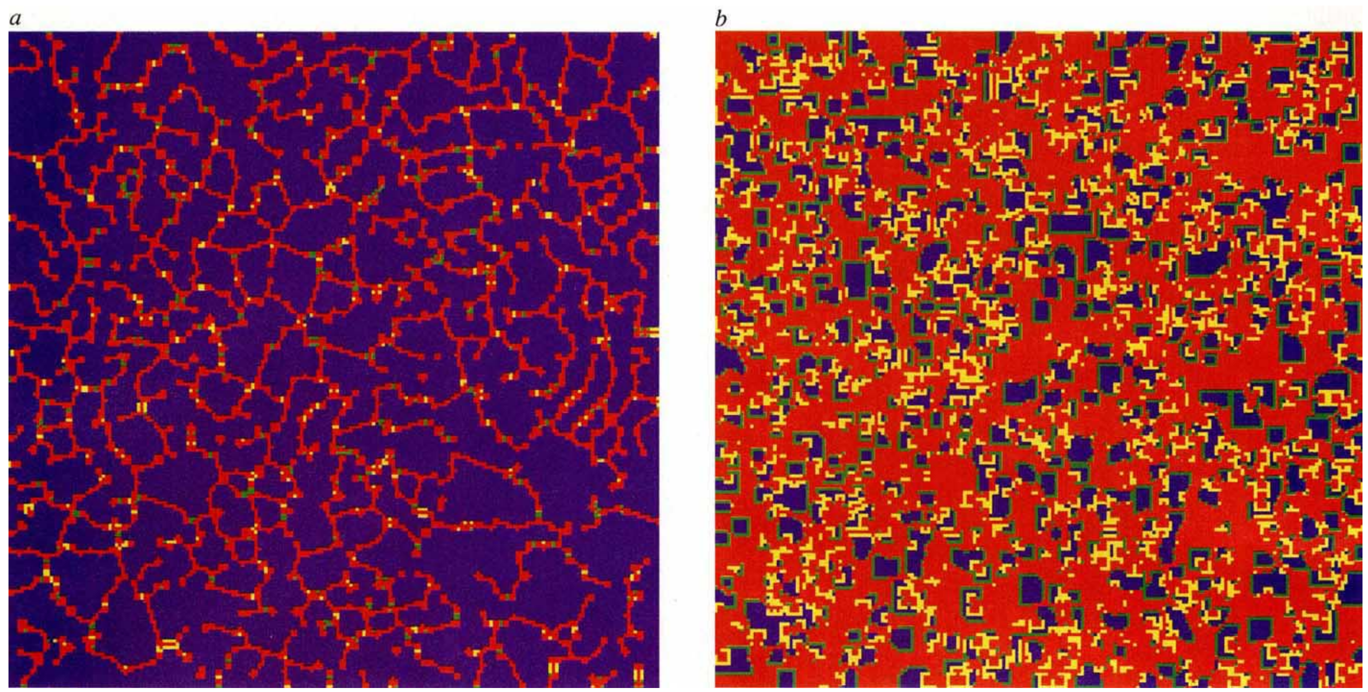
condition for the evolution of cooperation: $e_C + (1 - \frac{cN}{b}) > e_D$

Relation to kin selection: "Hamilton's rule"

$$(\frac{e_C + 1 - e_D}{N})b > c$$

"average excess relatedness" among C players

- Maintenance of cooperation in the Spatial Prisoner's Dilemma (cluster formation)

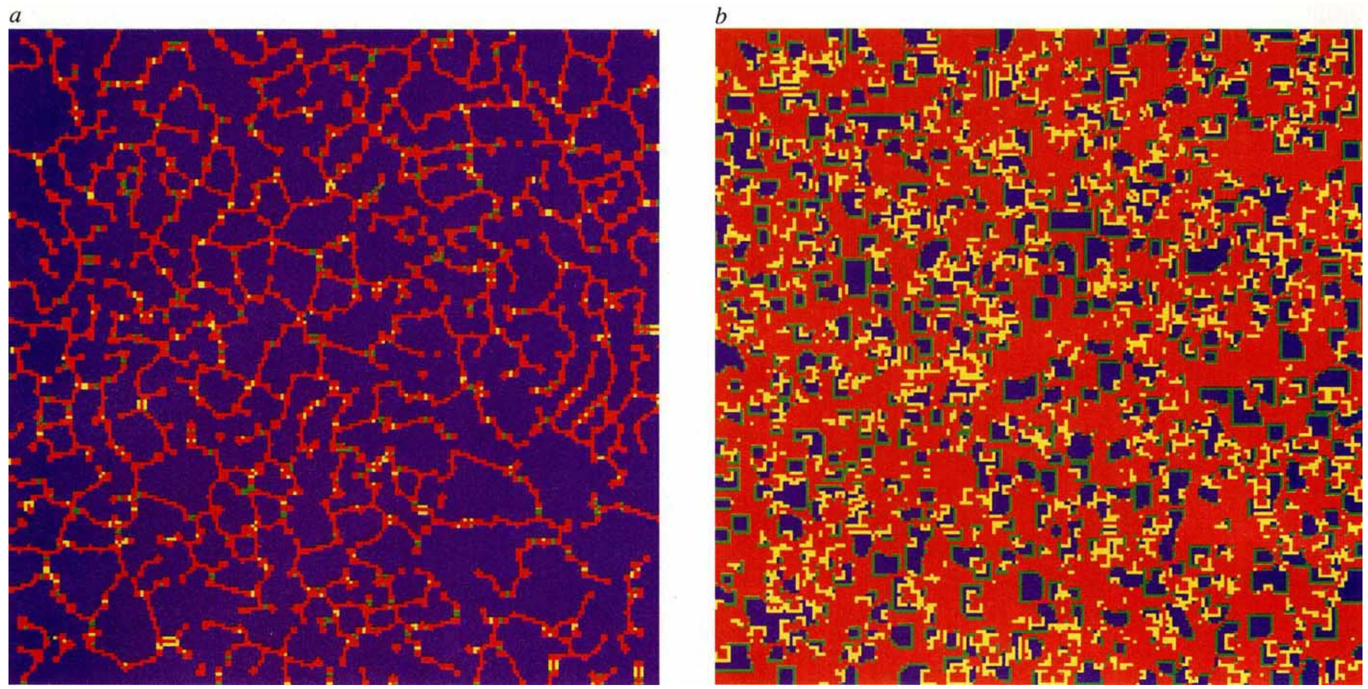


Nowak and May, Nature, 1992

- Example from Ackermann et al, Nature, 2008

Mechanisms for assortment ($e_C > e_D$): *Spatial structure*

- Maintenance of cooperation in the Spatial Prisoner's Dilemma (cluster formation)



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Phenotypic noise in *Salmonella typhimurium*

green: isogenic cells expressing virulence factor

grey: isogenic cells not expressing virulence factor

Nikki Freed, Ackermann lab, ETHZ

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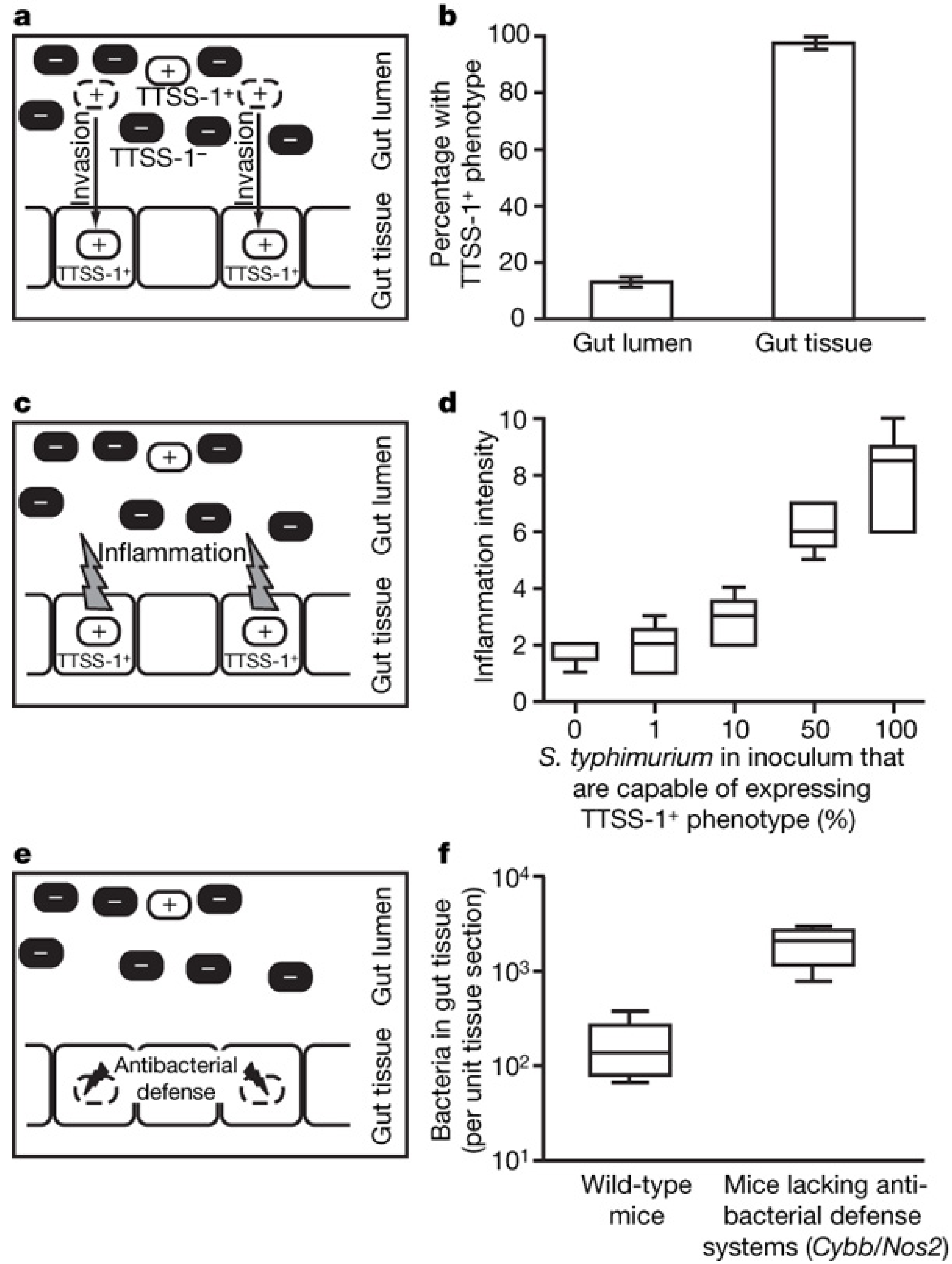
Phenotypic noise in *Salmonella typhimurium*

TTSS-1⁻ remains in lumen

TTSS-1⁺ migrates to gut wall

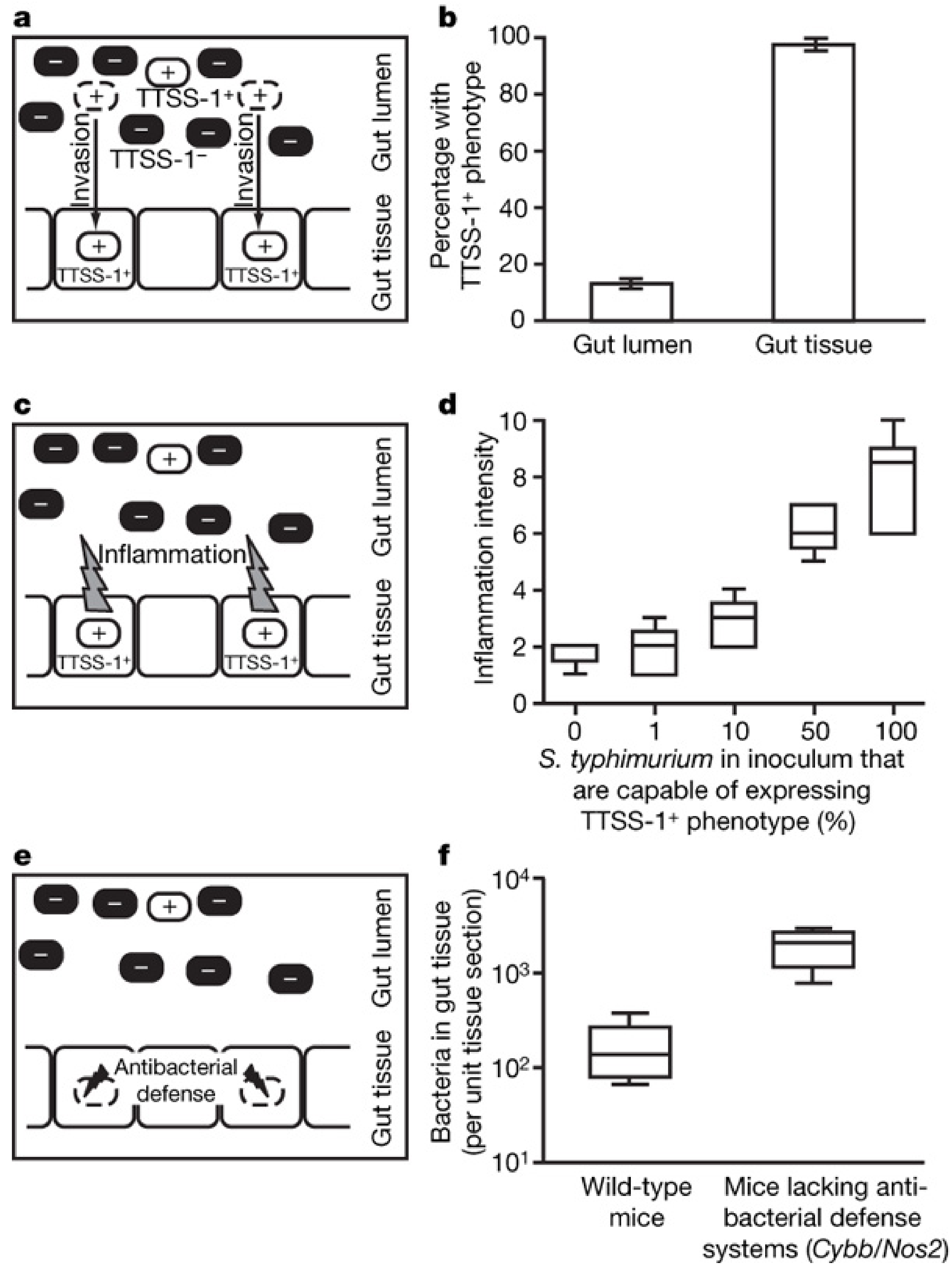


Phenotypic noise in *Salmonella typhimurium*

TTSS-1$^-$ remains in lumen

TTSS-1$^+$ migrates to gut wall

#TTSS-1$^+$ in gut wall correlates with inflammation (public good)



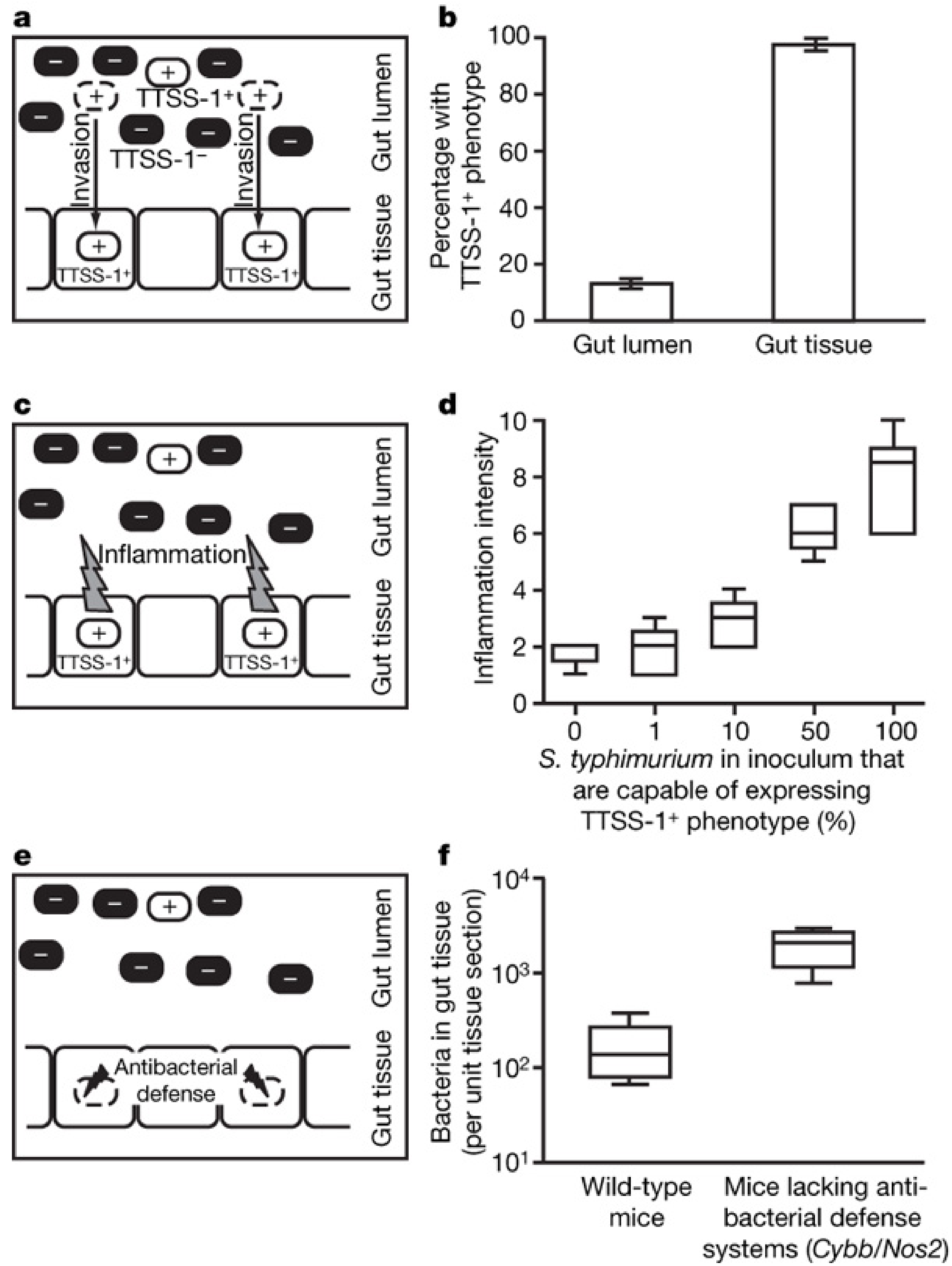
Phenotypic noise in *Salmonella typhimurium*

TTSS-1⁻ remains in lumen

TTSS-1⁺ migrates to gut wall

#TTSS-1⁺ in gut wall correlates with inflammation (public good)

TTSS-1⁺ in gut wall commit suicide



S. typhimurium public goods game

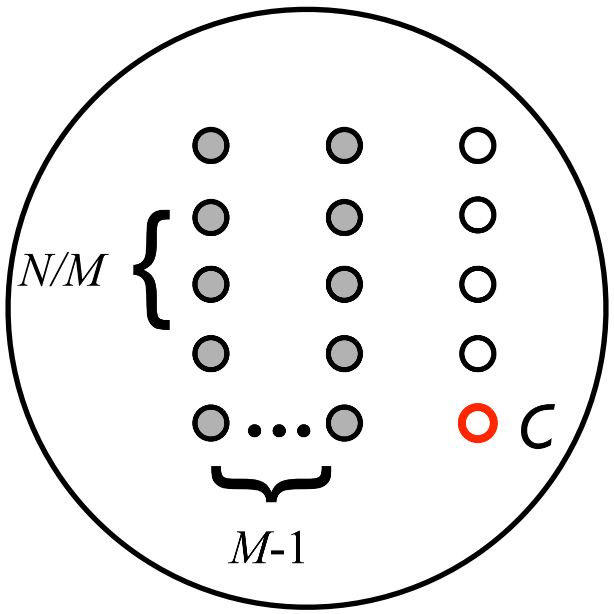
- single deme (single host) is seeded by *M* individuals, deme grows to population size *N*
- public goods game in each deme: D does nothing; with probability *q*, C commits suicide to provide benefit *b*
- payoffs in deme with *k* cooperators:

$$p_C(k) = (1-q)\left((k-1)qb + w\right)$$

$$p_D(k) = kqb + w$$

Spatial structure:
deme seeded by *M* individuals from global pool

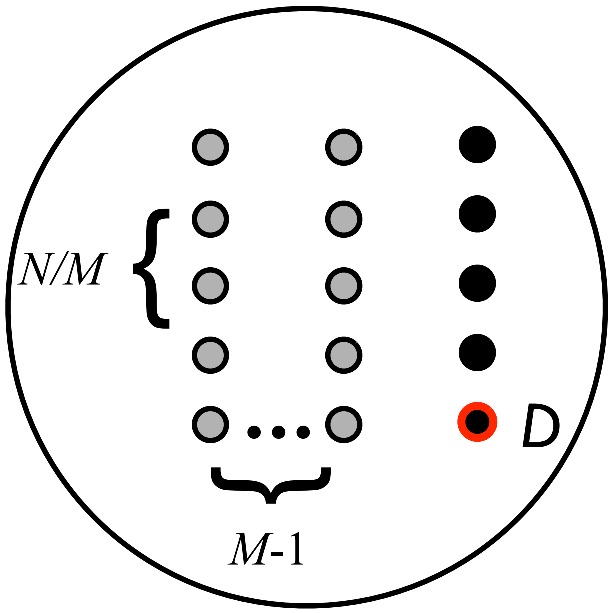
Average interaction environment of focal C:



$$e_C(x) = x(M-1)\frac{N}{M} + \frac{N}{M} - 1$$

x = global frequency of *C*

Average interaction environment of focal D:



$$e_D(x) = x(M-1)\frac{N}{M}$$

x = global frequency of *C*

Note: $e_C(x) - e_D(x) = \frac{N}{M} - 1 > 0$

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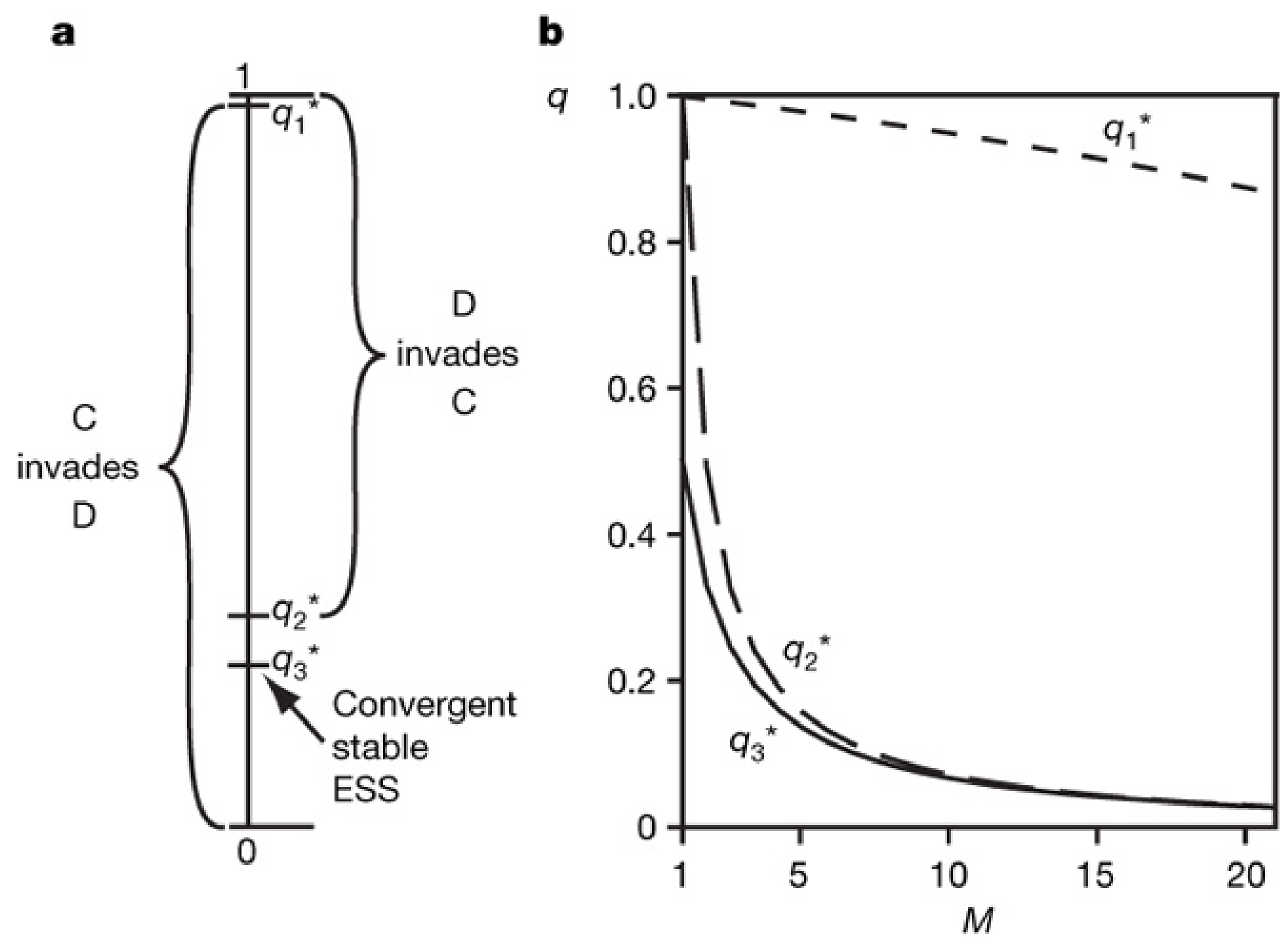
- payoffs in average interaction deme:

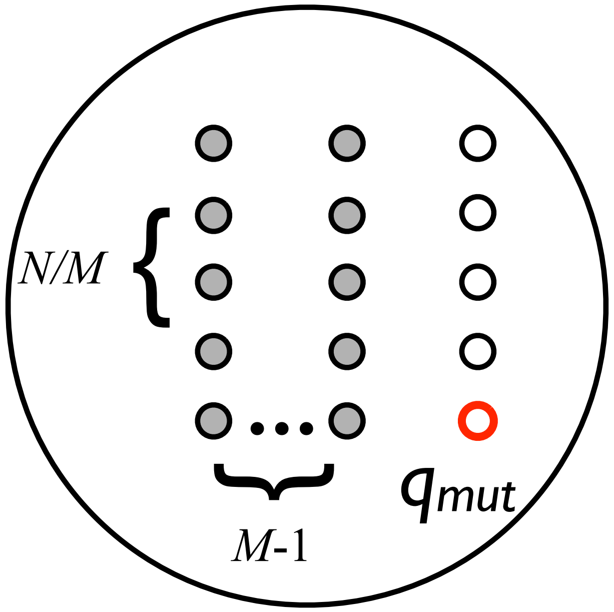
$$P_C = (1-q)((e_C(x)qb + w) \qquad\qquad P_D = e_D(x)qb + w$$



from Ackermann et al, Nature, 2008

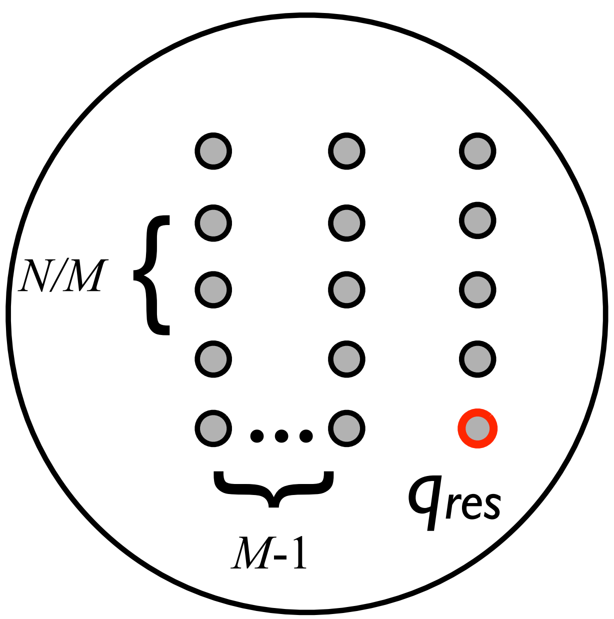
Adaptive dynamics: competition between different suicidal strategies q_{res} and q_{mut}

Average payoff to rare q_{mut}:



$$P_{q_{mut}} = (1 - q_{mut})\left[q_{mut} b(\frac{N}{M} - 1) + q_{res} b\frac{(M-1)N}{M}\right]$$

Average payoff to common q_{res}:



$$P_{q_{res}} = (1 - q_{res})\left[q_{res} b(N - 1)\right]$$

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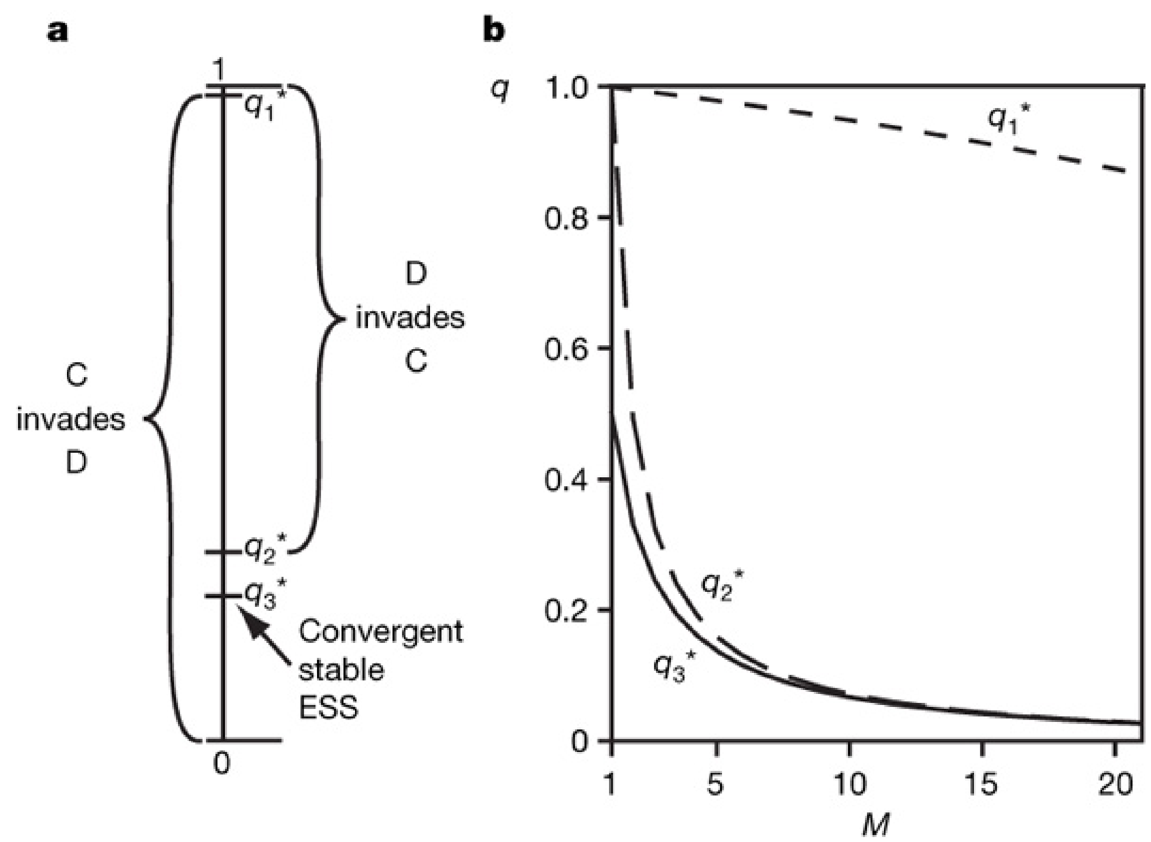

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Mechanisms for assortment : *Conditional behaviour*

Example (from Fletcher and Zwick 2007): Tit-for-Tat in the Iterated Prisoner's Dilemma

x = frequency of TFT, 1-x = frequency of AllD, N iterations

interaction environment of TFT player: xN cooperative acts

interaction environment of AllD player: x cooperative acts

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interaction environment of TFT player: xN cooperative acts

interaction environment of AllD player: x cooperative acts

Tit-for-Tat generates assortment between cooperators and cooperative behaviours of others

Conclusions for single-level selection models:

- Evolution of cooperation requires different interaction environments for cooperators and defectors (positive assortment between cooperative genotypes and cooperative behaviour of others) **Note:** equally applies to interspecific mutualism

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Conclusions for single-level selection models:

- Evolution of cooperation requires different interaction environments for cooperators and defectors (positive assortment between cooperative genotypes and cooperative behaviour of others) **Note:** equally applies to interspecific mutualism
- The concepts of kin selection (Hamilton's rule) and group selection (Price equation) are not necessary for understanding the evolution of cooperation; they are merely different fitness accounting techniques.
- **The biological problem:** understanding the mechanisms that lead to assortment (spatial structure, conditional behaviour, …)

2. Multi-level selection models

Traditional group selection models:

- Group properties derived from properties of the individuals in a group (e.g. "productivity"=average individual fitness)
- Price equation: essentially a type of accounting of individual fitness

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- Price equation: essentially a type of accounting of individual fitness

"True" group selection models:

- Need birth-death process at both the individual and the group level
- Basic assumption: population consists of "groups of individuals" (e.g. groups of individual pathogens defined as those living in a single host; tribes of hunter-gatherers,...)

A generic group selection model

Individuals can have types {1,2,...k}

A group is specified by a vector $x = (x_1, \ldots, x_k)$

$x_i =$ number of $i-$ individuals in the group

Basic quantity:

$$\Theta(x,t) = \text{ number of } x-\text{groups in the population at time } t$$

e.g. $G(t) = \int \Theta(x,t)dx = \text{ number groups at time } t$

$N_i(t) = \int x_i\Theta(x,t)dx = \text{ number of type } i \text{ individuals at time } t$

Goal: understand the dynamics of $\Theta(x,t)$

Individual-level events: birth, death (and migration) of individuals

$$b_i(x,t) = \text{ birth rate of } i \text{ individuals in groups of composition } x$$

$$d_i(x,t) = \text{ death rate of } i \text{ individuals in groups of composition } x$$

Group level events: fissioning and extinction of groups (and possibly fusion)

$$f(x,t) = \text{ fissioning rate of } x \text{ groups}$$

$$h(u,x) = \text{ fissioning density: distribution of groups formed when an } x \text{ group is fissioning}$$

$$e(x,t) = \text{ extinction rate of } x \text{ groups}$$

Note:

- all rates can be affected by interactions, group composition, total number of individuals and groups, etc.
- fissioning and extinction rates of groups can be affected by games between groups (e.g. in cultural evolution)

“Master equation” for group selection:

$$\frac{\partial \Theta(x,t)}{\partial t} + \sum_{i=1}^{k} \frac{\partial \left(\Theta(x,t)(b_i(x,t) - d_i(x,t)) \right)}{\partial x_i} = \int f(y,t)\Theta(y,t)h(x,y)dy - (e(x,t) + f(x,t))\Theta(x,t)$$

dynamics due individual level events

dynamics due to group level events

Definition: A trait evolves by group selection if it establishes itself when group-level events are present in the model, and does not establish itself in the same model when they are absent.

Example: evolution of cooperation in hunter-gatherer tribes

Basic assumptions:

- Defectors have higher birth rates than cooperators in every tribe
- Larger tribes, and tribes with a larger proportion of defectors, are more likely to fission
- Smaller tribes, and tribes with a larger proportion of defectors, are more likely to die of extinction.

Video of a PDE solution of the model

Video of a stochastic version of the model

Figure 1a

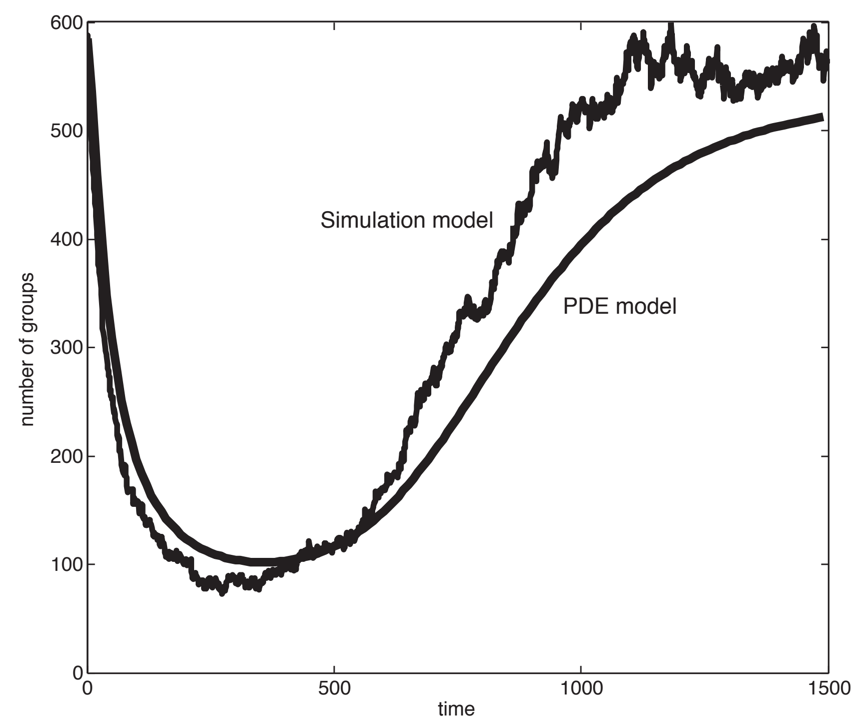
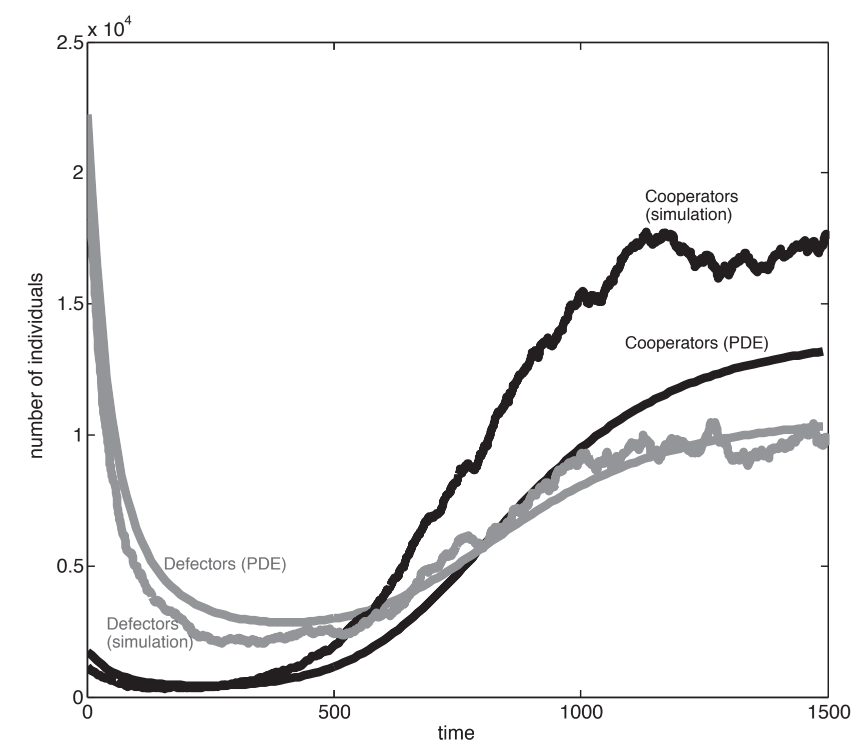


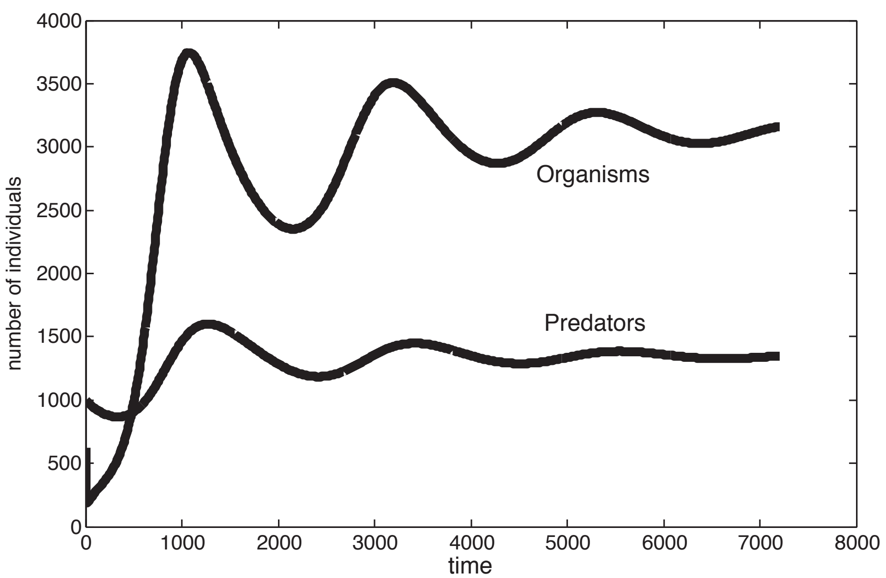
Figure 1b

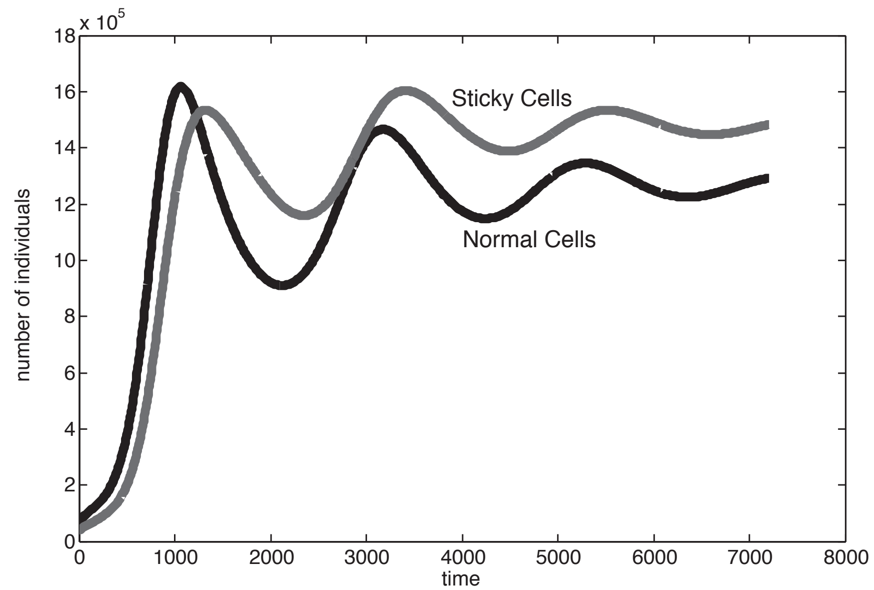


Example: evolution of "multicelluarity" (sticky cells)

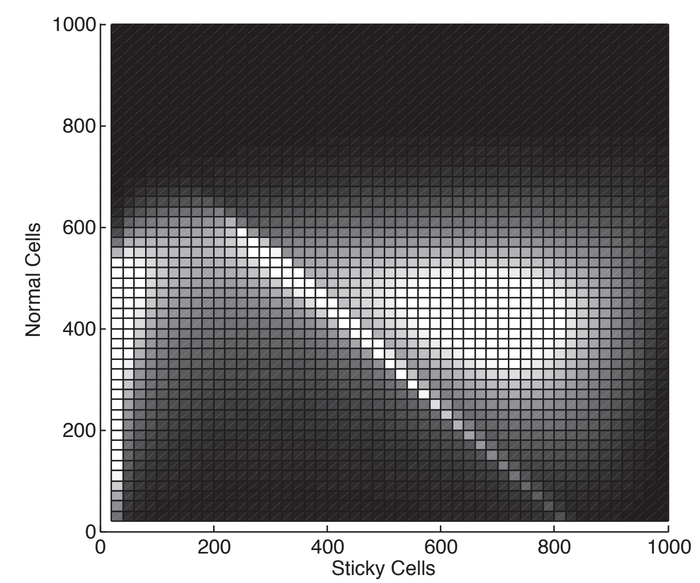
Basic assumptions:

- Two kinds of cells: "sticky" and "normal"
- Groups = "organisms" consisting of a number of sticky and normal cells
- Normal cells reproduce at a faster rate than sticky cells
- Stickier organisms are less likely to fission and more likely to fuse
- Smaller organisms are more likely to be eaten by predators





equilibrium configuration



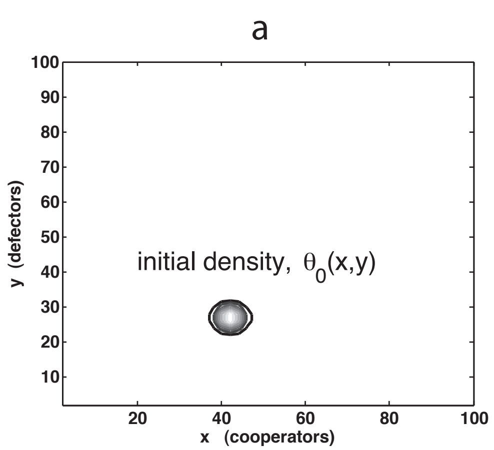
Example: evolution of cooperation in groups playing public goods games

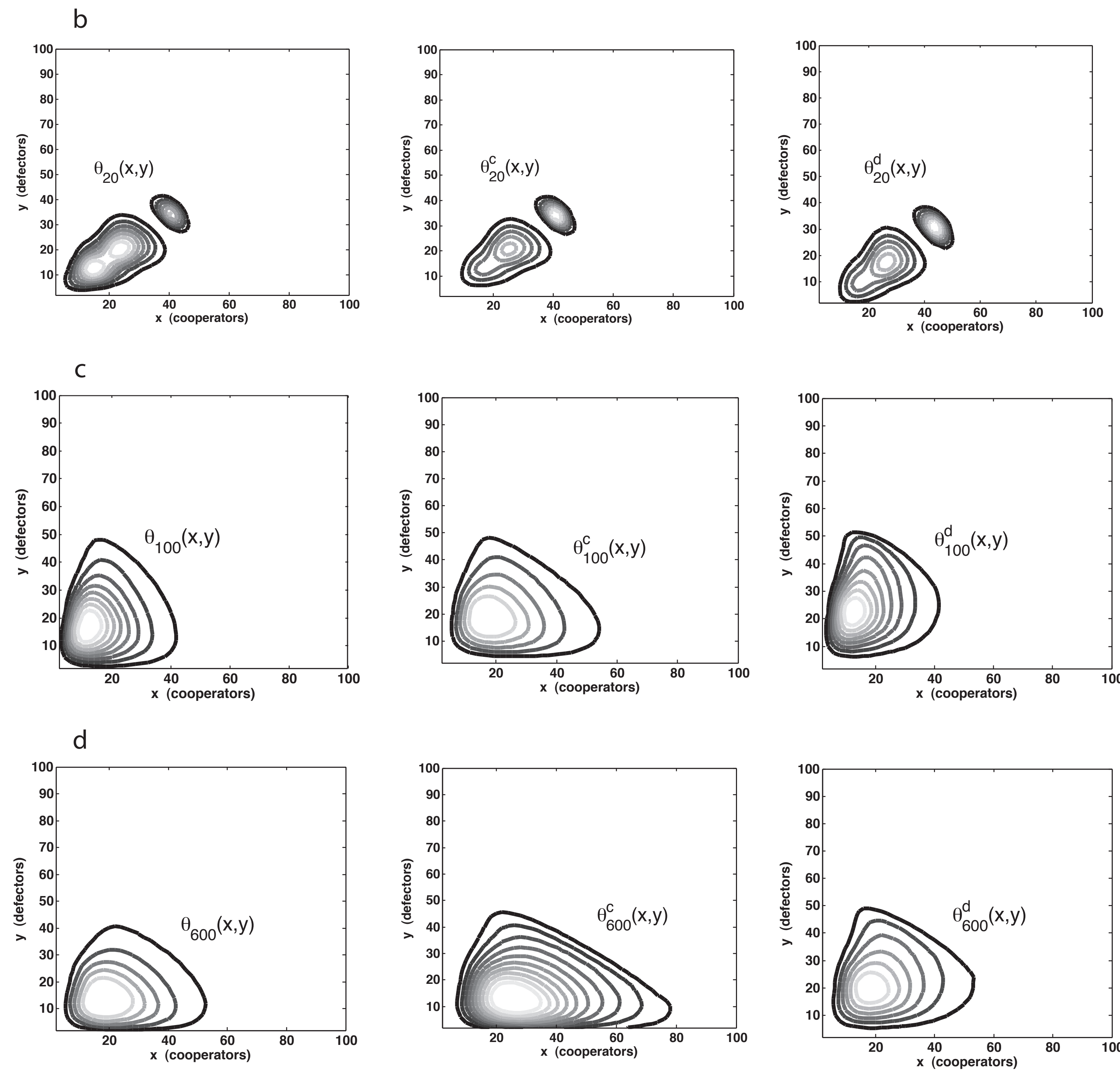
Basic assumptions:

- Groups consist of Cooperators and Defectors
- Individual birth rates are given by payoffs from public goods game (logistic death rates)
- Larger groups and groups with larger proportions of Cooperators are less likely to go extinct
- Groups with larger proportions of Defectors cooperators are more likely to fission

Dynamics of assortment

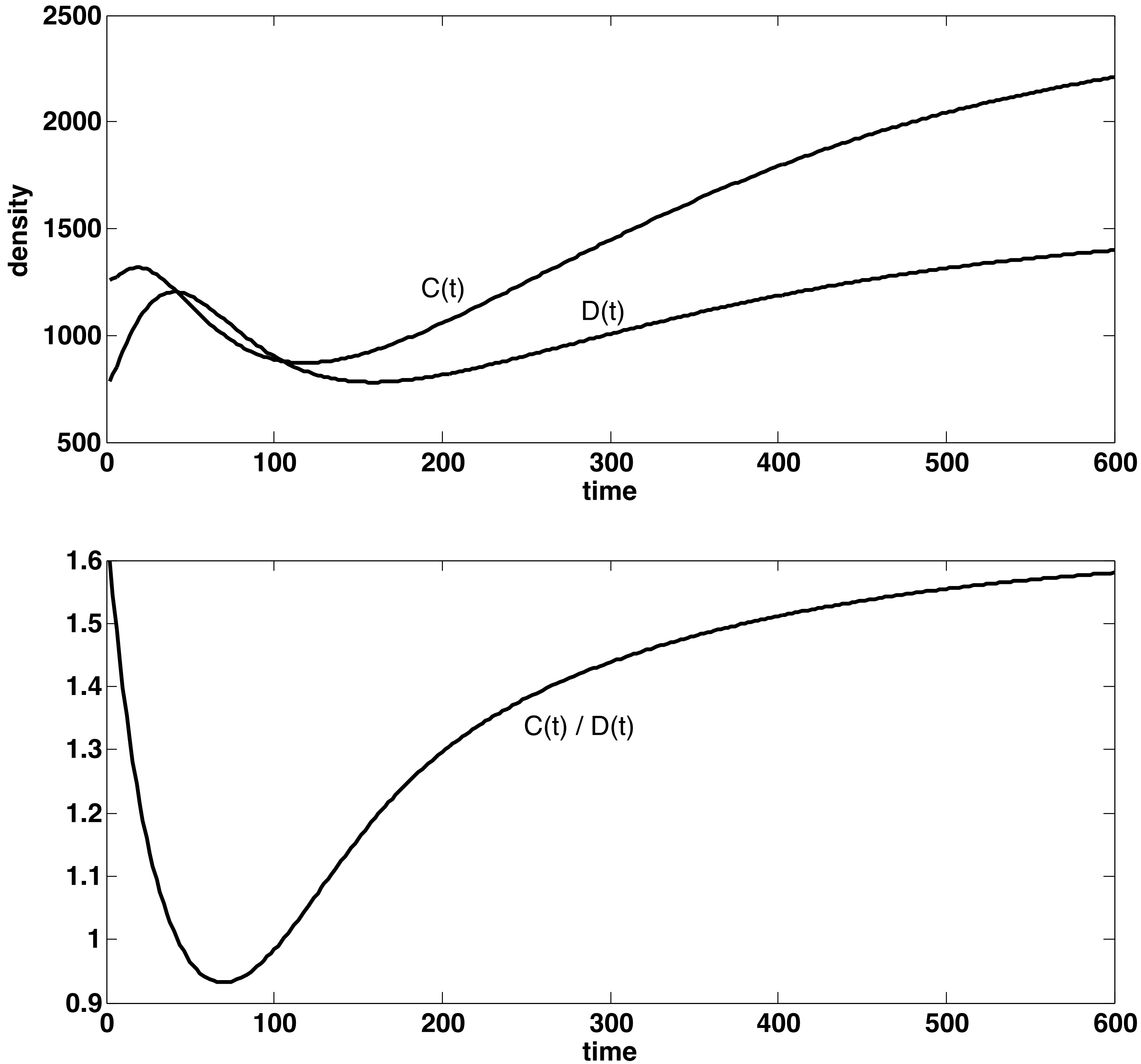
Initial density | Total density | Density seen by average Cooperator | Density seen by average Defector





Cooperation maintained
due to dynamics of assortment

- Assortment (or relatedness) are instantaneous measures that can only predict short term dynamics
- Dynamics of assortment (or relatedness) are determined by group level events and are needed to predict long-term dynamics



C(t) = cooperators at time t
D(t) = defectors at time t

Summary

Single-level selection models:

- Evolution of cooperation requires different interaction environments for cooperators and defectors (positive assortment between cooperative genotypes and cooperative behaviour of others)
- The concepts of kin and group selection are not necessary for understanding the evolution of cooperation
- The biological problem is to understand the mechanisms that lead to assortment (spatial structure, conditional behaviour, …)

Summary

Single-level selection models:

- Evolution of cooperation requires different interaction environments for cooperators and defectors (positive assortment between cooperative genotypes and cooperative behaviour of others)
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Multi-level selection models:

- Require birth and death processes at multiple levels (e.g. at the individual and at the group level)
- In such models, events that affect birth and death rates at the group level must be taken into account, e.g to understand the dynamics of assortment
- However, assortment at the individual level is in general not enough to understand the dynamics cooperation in multi-level models (e.g. when there are games between groups)