On the evolution of reciprocal cooperation

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Biodiversity and Environment: Viability and Dynamic Games Perspectives
Montreal, November 4-8, 2013

On the non-evolution of reciprocal cooperation

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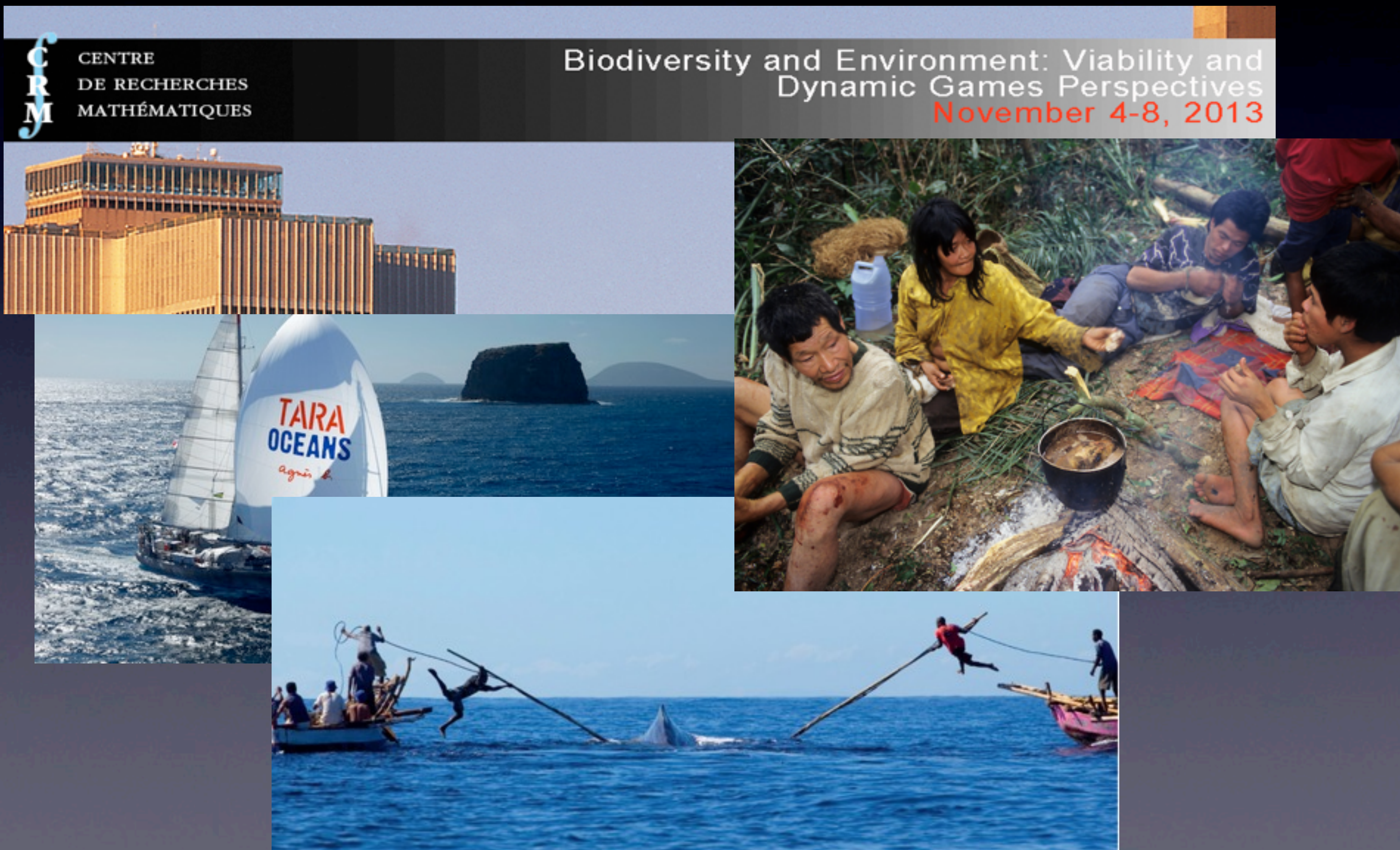
Humans do cooperate



Level of *organization*

- People act so as to guarantee that the whole *group* functions efficiently
- The *group*, not the individual, is the right level of *organization*

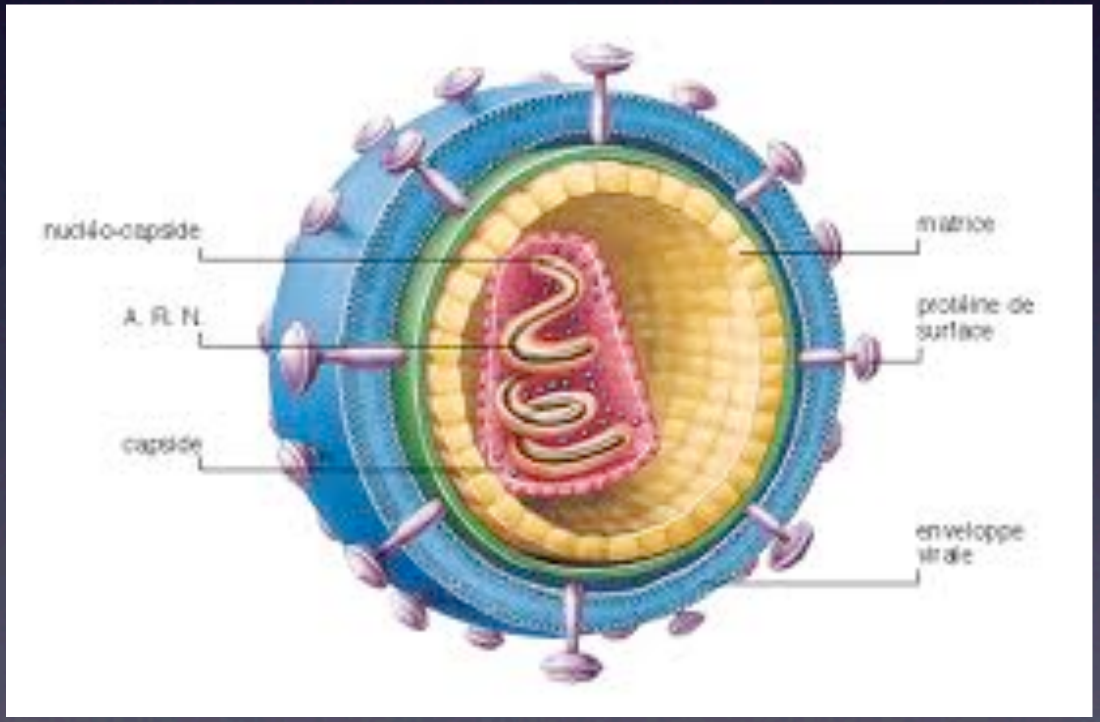
The usual debate

- Are humans altruists or mutualists?
  Do people *really* sacrifice themselves for the group?
- If human cooperation is mutualistic,
  then its existence is trivial for evolutionary biologists,
  as everyone benefits
- This debate misses a key point

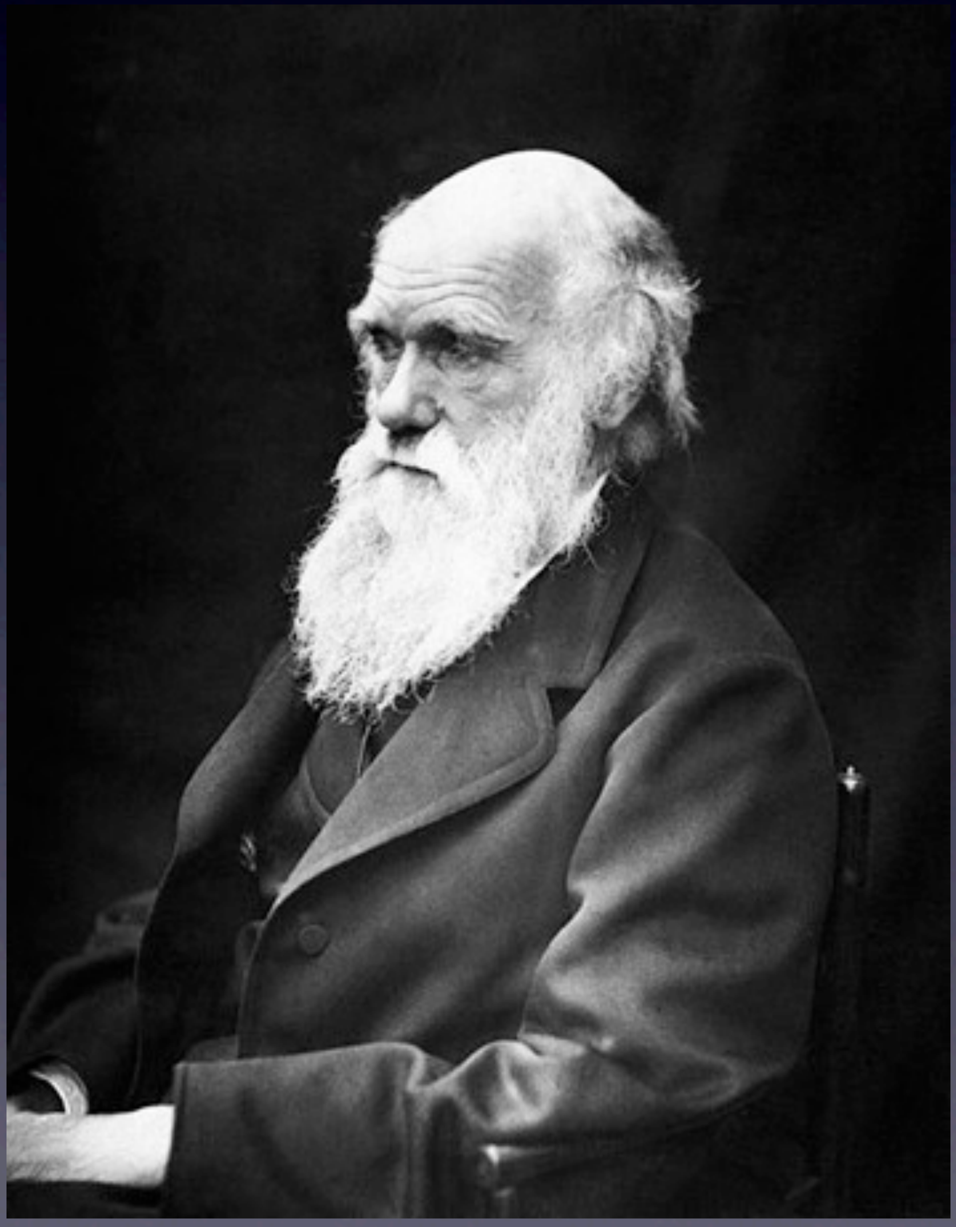
see West et al. 2011

The origin of organization

Where does functional *organization* come from?
(in a world without final causes)



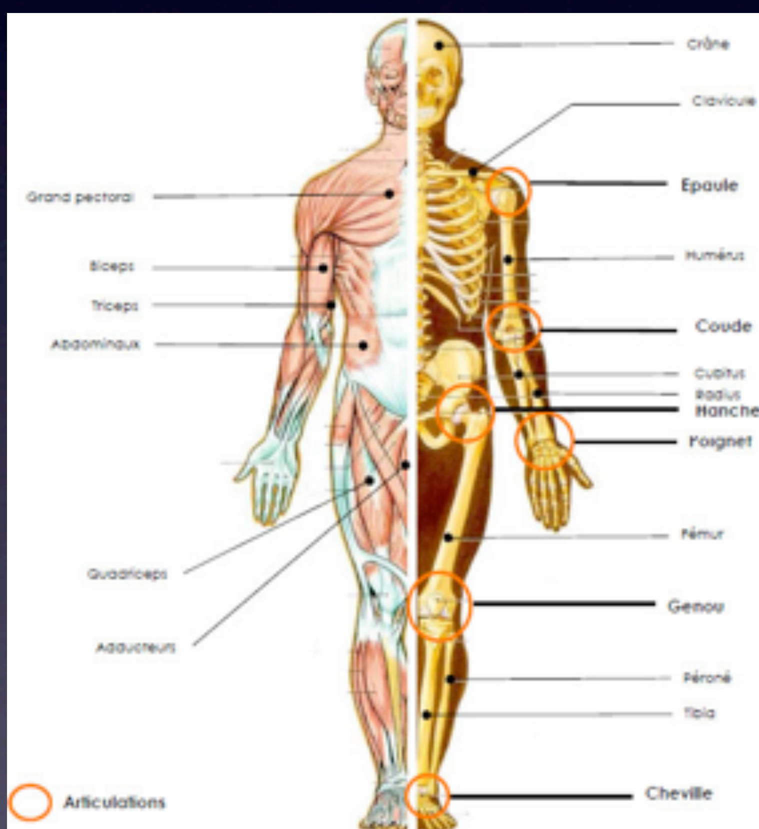
The origin of organization



Functional organization comes from *natural selection*

Natural selection acts on « *replicators* »

What about large scale organization?



Major transitions

Maynard-Smith and Szathmary 1995

Kin selection

Individuals interact with genetically related partners

Natural selection acts on the group

Queller (1997) calls this a *fraternal* transition

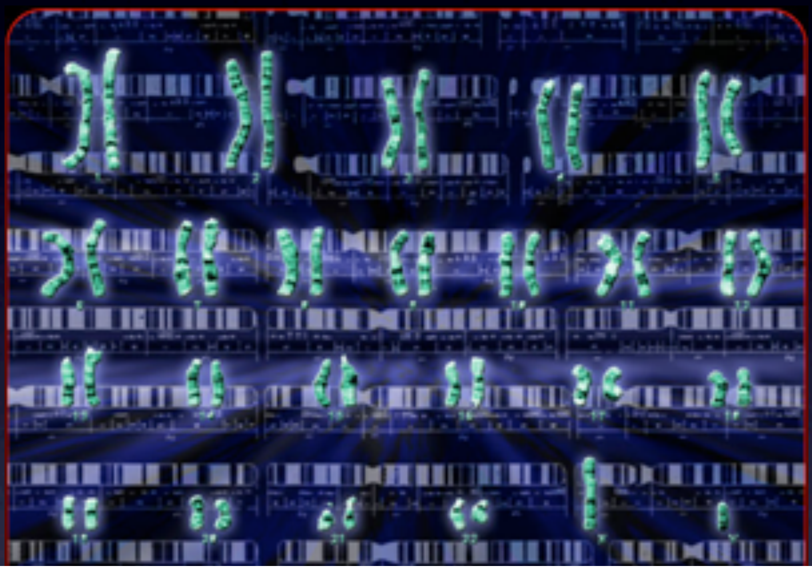
Hamilton 1964 ; Maynard-Smith and Szathmary 1995 ; Queller 1997

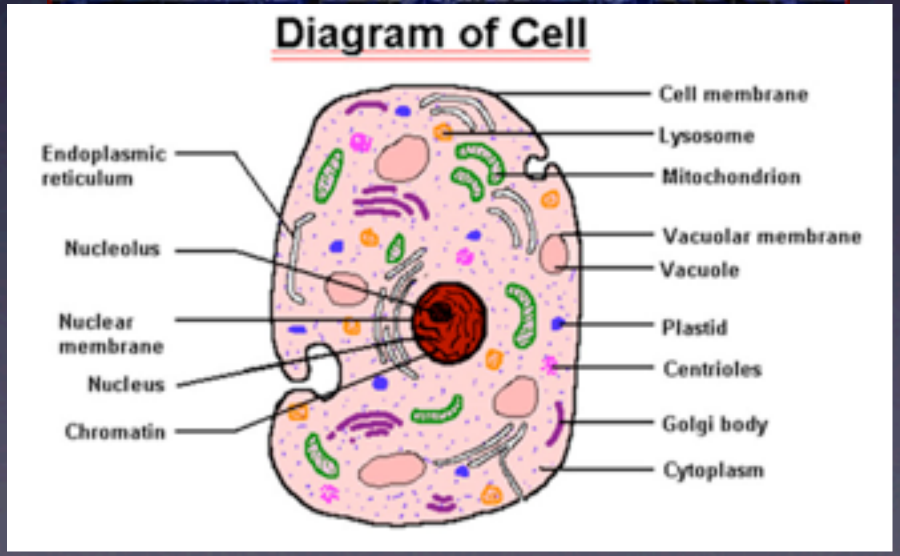
Common interest

Individuals have their fate linked (e.g. by co-transmission and/or fair meiosis)

Individual properties become group properties, hence *natural selection acts on the group*

Queller (1997) calls this an *egalitarian* transition





Maynard-Smith and Szathmary 1995 ; Queller 1997

Level of selection

- In either case, the *level of organization* is scaled up because the *level of selection* is also scaled up
- The new *level of selection* comes
  as a result of a new *level of heritability*

Maynard-Smith and Szathmary 1995 ; Queller 1997

(mistaken) Application to the human case

- Human groups have functional features
- Natural selection must have acted *on groups* to shape these features
- *Culture* must play a key role because only cultural traits can be heritable at the group level

Boyd, Richerson, Henrich, Gintis, Fehr, Fischbacher, Bowles, Allison, etc.

Reciprocity is an alternative

Cooperation in individual A
causes cooperation in individual B

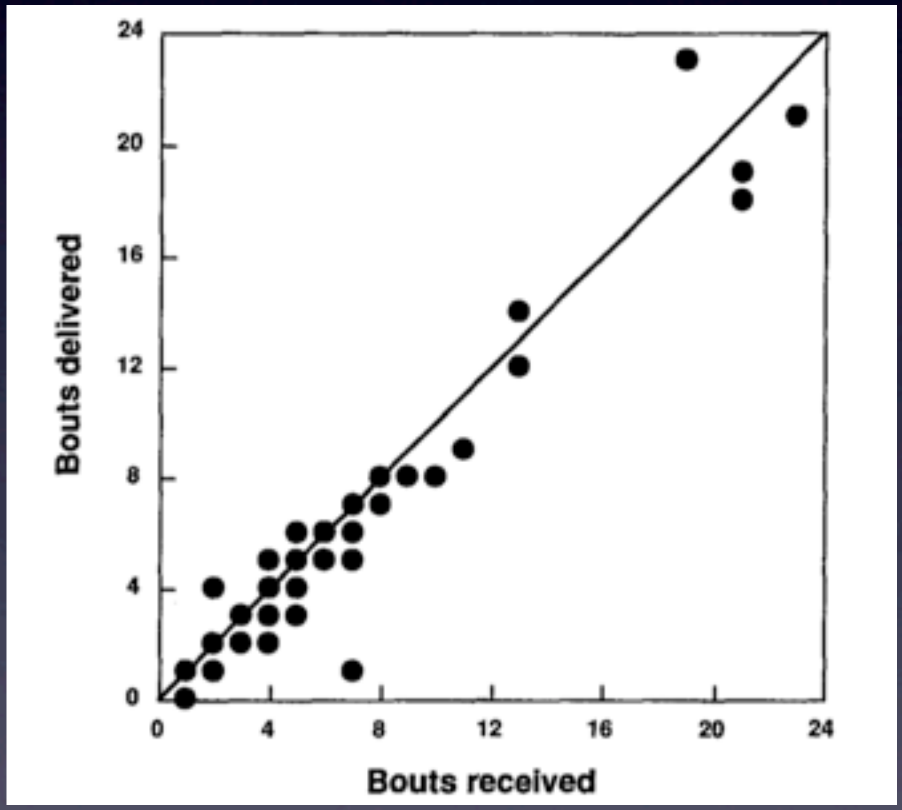
Trivers 1971; Axelrod and Hamilton 1981; etc.

Reciprocity *sensu lato*

- *Direct reciprocity*:
  back and forth exchanges between A and B
- *Indirect reciprocity* and *partner choice:*
  A helps B and receives benefits from C in return
- *Punishment*:
  A helps B and avoids being punished by C

Nowak & Sigmund 1992, 1993 ; Leimar & Hammerstein 2001 ; Boyd & Richerson 1992 ; etc.

Examples



Hart & Hart 1992

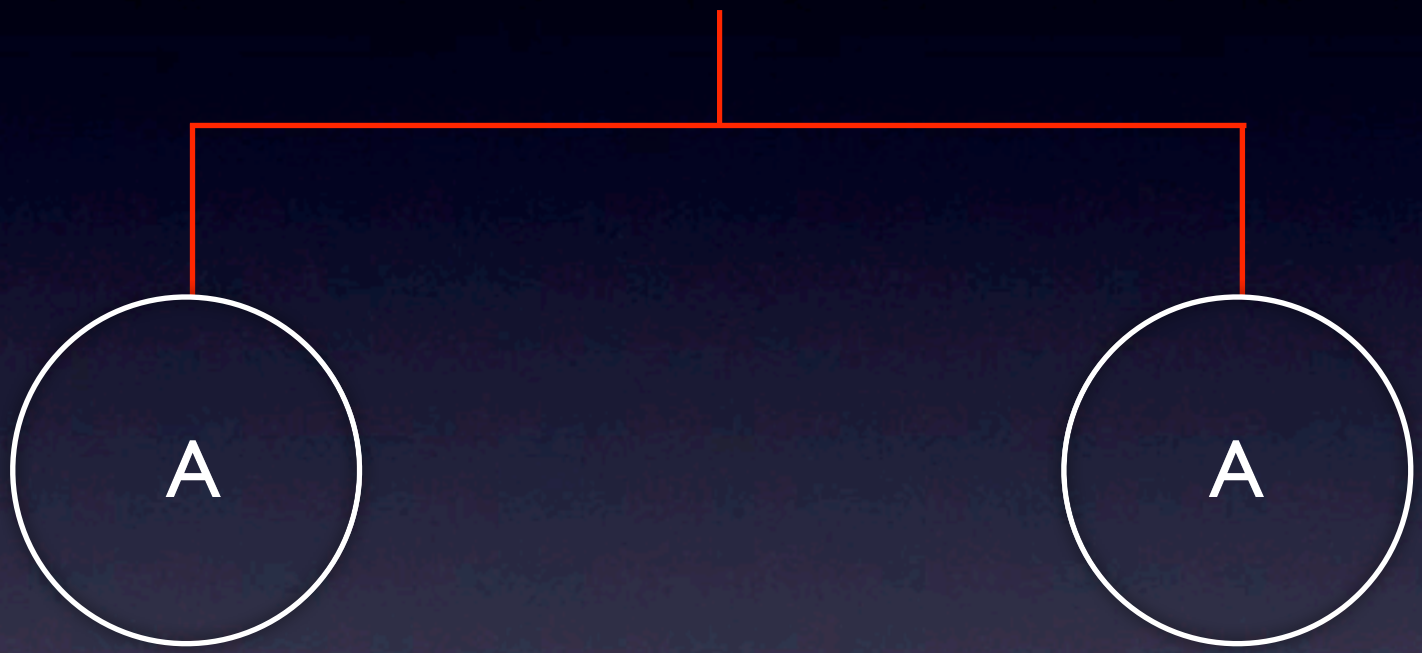
Examples

Gurven 2004

Alvard and Nolin 2002

see also e.g. Barclay and Willer 2007 ; etc.

The fraternal transition



Cooperation is made adaptive
by *genetic relatedness*

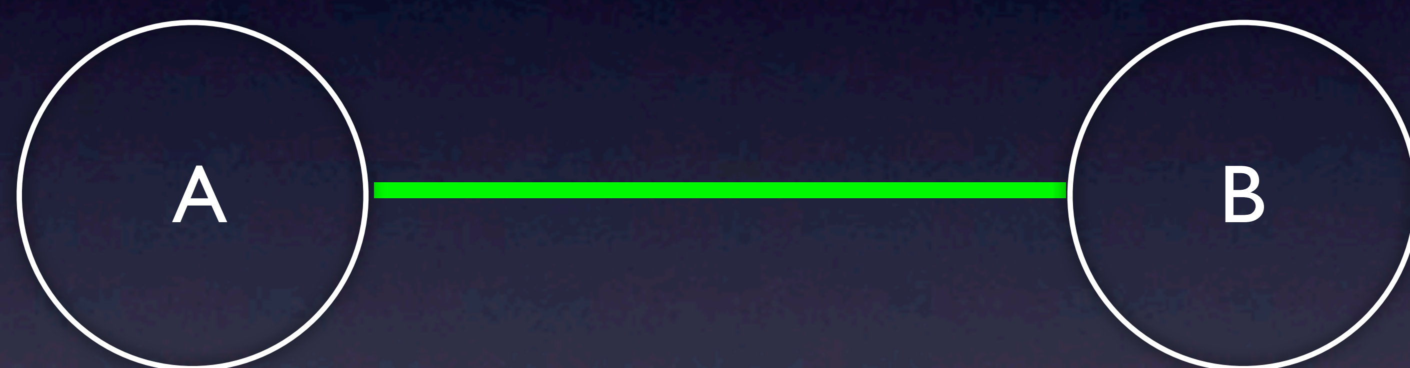
Queller 1997

The egalitarian transition

Cooperation is made adaptive
by *objective common interest*

Queller 1997

The egalitarian transition



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Cooperation is made adaptive
by *objective common interest*

Queller 1997

The liberal transition

Cooperation is made adaptive
by ***individuals themselves***

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and yet...

Reciprocity is rare

- Reciprocal exchanges are seldom observed outside humans
- Each purported example is subject to controversy

Connor 1986 ; Hammerstein 2003 ; West et al. 2007
Bergmuller et al. 2007 ; Clutton-Brock, 2009 ; Leimar & Hammerstein 2010 ; etc.

Reciprocity is *extremely* rare

Genes in a genome,
cells in a body,
ants in a colony,
act in a coordinated fashion for a common benefit

because they are genetically related or have a common interest

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Reciprocity is *extremely* rare

In principle, with reciprocity, all individuals on earth could be cooperating together in a similar fashion

but they generally don't

Connor 1986 ; Hammerstein 2003 ; West et al. 2007
Bergmuller et al. 2007 ; Clutton-Brock, 2009 ; Leimar & Hammerstein 2010 ; etc.

Three questions

- Why is reciprocity so rare outside humans?
- Why is it sometimes present?
- Why is it so developed in humans?

Three questions

- Why is reciprocity so rare outside humans?
- Why is it sometimes present?
- Why is it so developed in humans?

A matter of cognitive complexity?

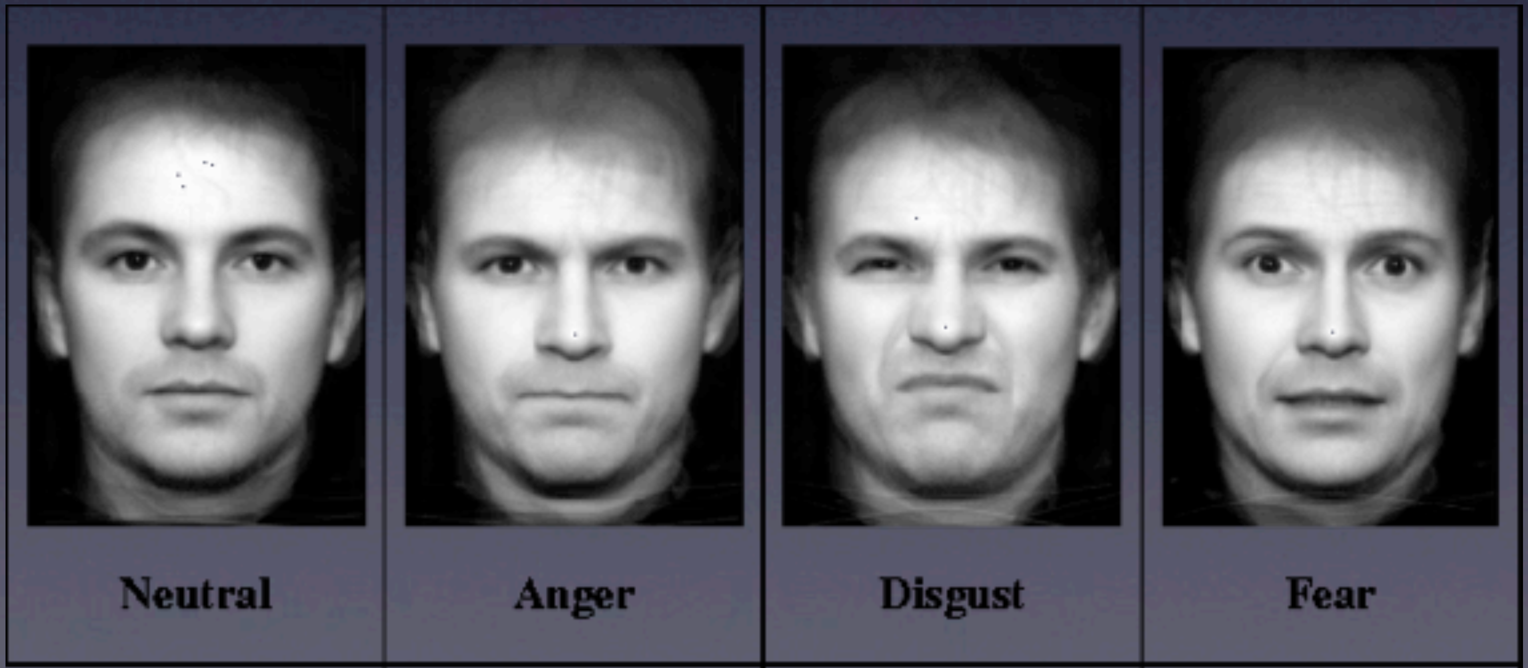
« cognitive limitations such as temporal discounting, numerical discrimination and memory make reciprocity difficult for animals »

Stevens & Hauser 2005

see also Hammerstein 2003

A matter of cognitive complexity?

896543326678
+543378876 = ?



A matter of cognitive complexity?

The complexity argument entails a confusion between proximate and ultimate causes

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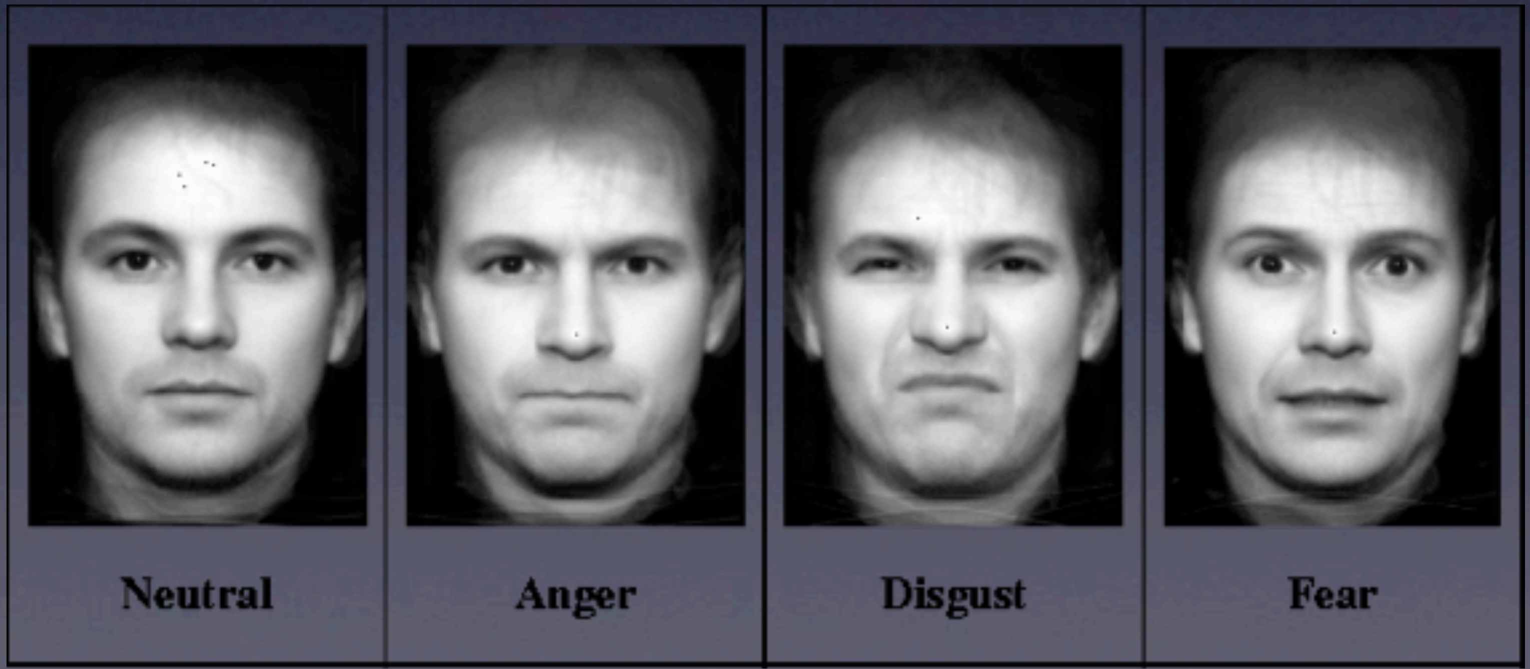
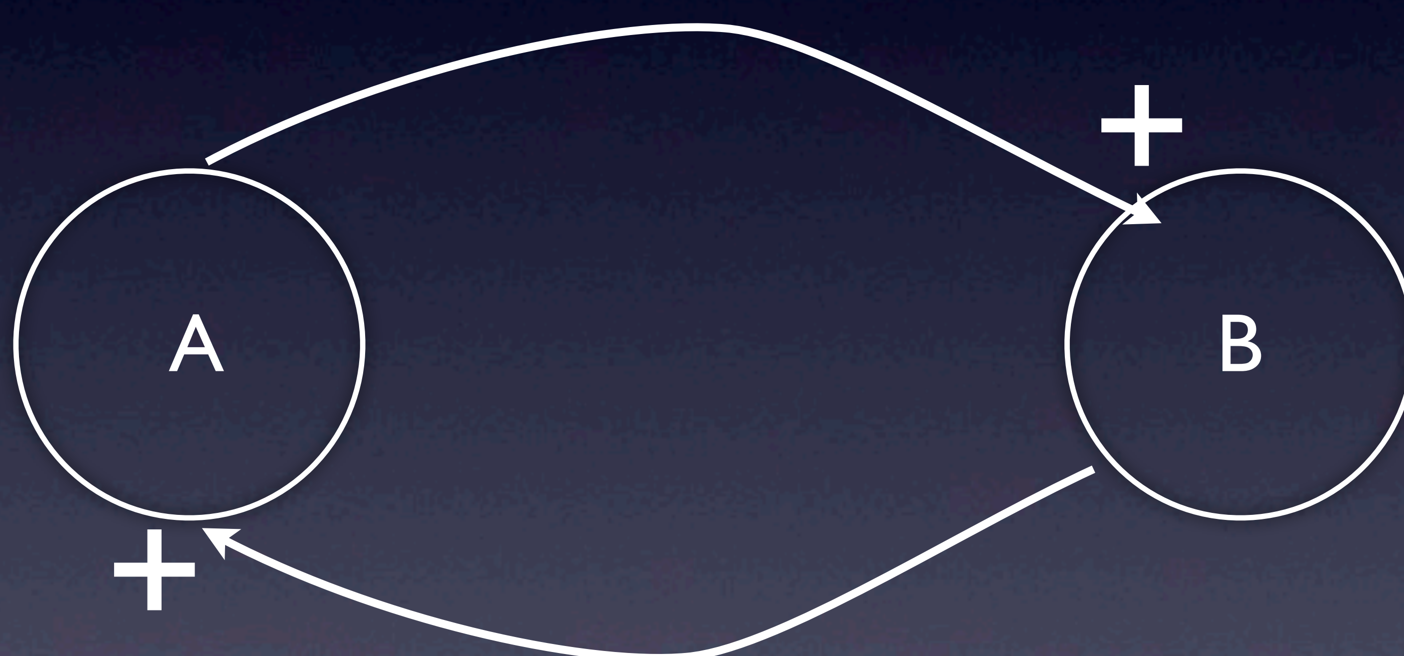


Hypothesis:

The problem is that reciprocity is *circular*



A's cooperation
is adaptive because it triggers
B's cooperation

B's cooperation
is adaptive because it triggers
A's cooperation

Circularity is a problem for *evolution*

- Being a reciprocator is adaptive when others are reciprocators, i.e. *reciprocity is an adaptation to itself*
- Reciprocity may be evolutionarily *stable*, but how can it *evolve*?

Why does reciprocity evolve in many models?

- Most models follow
  an (implicit) facilitating assumption
- With more natural assumptions,
  reciprocity is very unlikely to evolve

Usual models

individuals are characterized by two traits:

- γ_c : cooperative tendency after cooperation
- γ_d : cooperative tendency after defection

γ_d \ γ_c	*0*	*1*
0	*AllD*	*TFT*
1	*Perv.*	*AllC*

→ a *single* mutation* transforms a defector into a reciprocator

e.g. Nowak and Sigmund 1992; etc.

The analysis

- Evolution follows a Moran process,
  i.e. every time step one individual dies
  and is replaced by the offspring of another
  (with a probability proportional to fitness)
- The population is characterized by the number of individuals playing each of the four strategies.
- Evolution is a markov process in the 4-simplex

Fudenberg & Imhoff 2010

The analysis

- The mutation rate is assumed to be very small, hence the population is almost always in a homogeneous state
- Evolution is a markov process on the vertices of the 4-simplex

Fudenberg & Imhoff 2010

The analysis

Transition probability from state s_1 to state s_2 :

$$u_{12} \times p_{12}$$

Karlin & Taylor 1975 ; Fudenberg & Imhoff 2010 ; Nowak et al. 2004 ; Garcia and Traulsen 2012

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Transition probability from state s_1 to state s_2 :

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probability of mutation from strategy s_1 to strategy s_2

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The analysis

Transition probability from state s_1 to state s_2 :

$$u_{12} \times p_{12}$$

probability of mutation from strategy s_1 to strategy s_2

probability of fixation of a single mutant playing strategy s_2
in a population of N-1 individuals playing s_1

$$p_{12} = \frac{1}{1 + \sum_{k=1}^{N-1} \prod_{n=1}^{k} \frac{F(s_1, s_2, N-n)}{F(s_2, s_1, n)}}$$

Karlin & Taylor 1975 ; Fudenberg & Imhoff 2010 ; Nowak et al. 2004 ; Garcia and Traulsen 2012

The analysis

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How long to reach AllC for the first time?

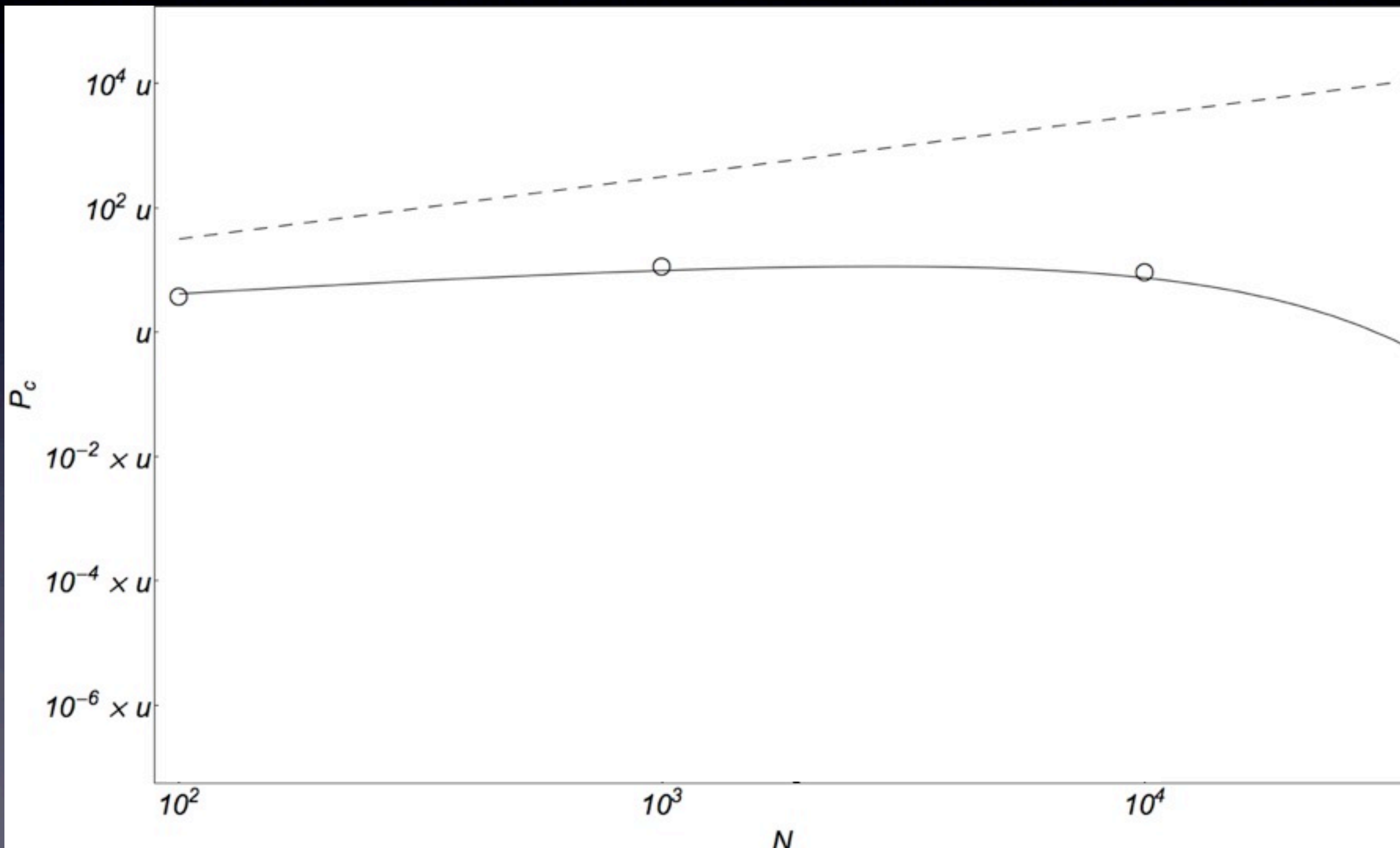
Invasion barrier

- A single reciprocating individual
is always counter-selected

- But several reciprocating individuals *together*
can become favored

- Reciprocity needs to overcome an *invasion barrier*,
which can occur with genetic drift (e.g. Nowak et al. 2004)

Results



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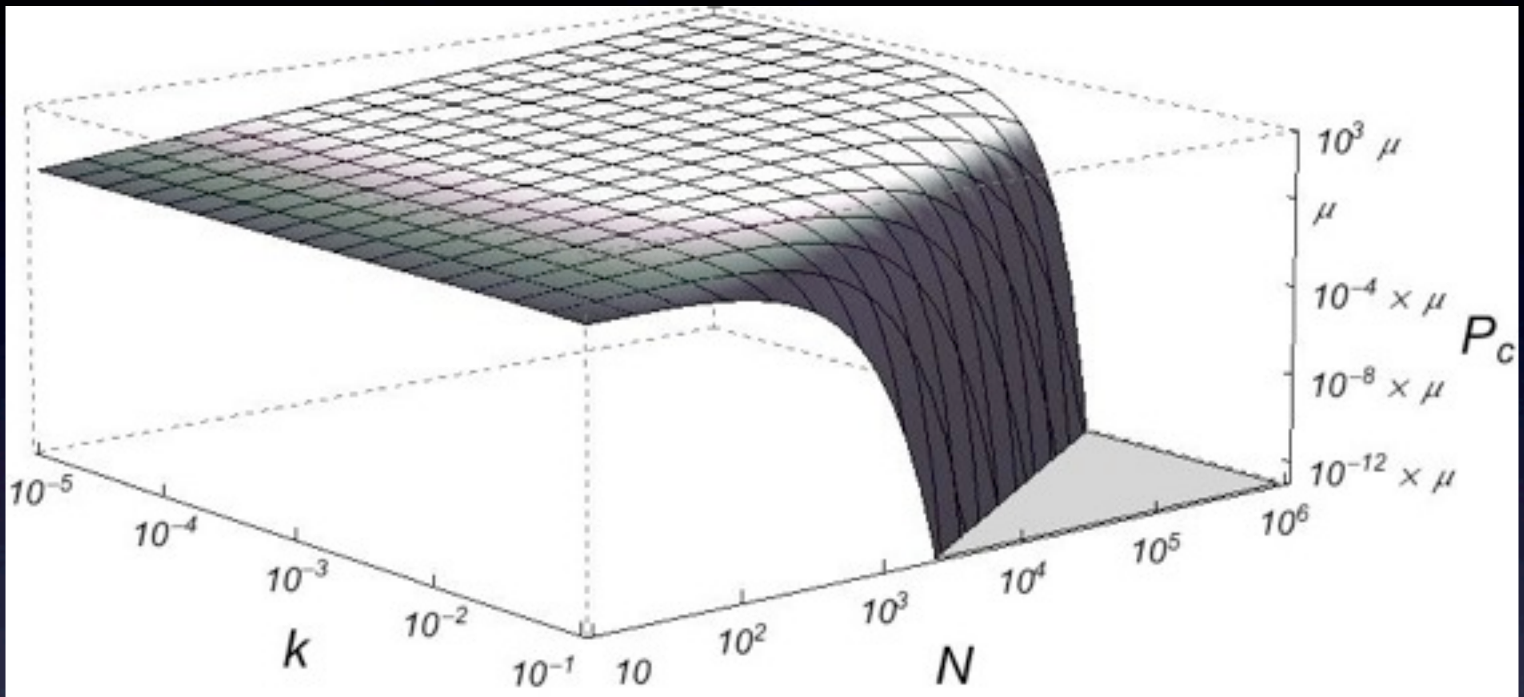

$10^3\ \mu$
μ
$10^{-4} \times \mu$
P_c
$10^{-8} \times \mu$
$10^{-12} \times \mu$
10^{-5}
10^{-4}
10^{-3}
10^{-2}
10^{-1}
k
10
10^2
10^3
10^4
10^5
10^6
N

A biological problem with this model

γ_d \ γ_c	*0*	*1*
0	*AllD*	*TFT*
1	*Perv.*	*AllC*

A biological problem with this model

unable to cooperate *at all*

γ_d \ γ_c	*0*	*1*
0	*AllD*	*TFT*
1	*Perv.*	*AllC*

A biological problem with this model

unable to cooperate *at all*

Y_d \ Y_c	*0*	*1*
0	*AllD*	*TFT*
1	*Perv.*	*AllC*

(i) cooperates and (ii) responds to others' cooperation

A biological problem with this model

unable to cooperate *at all*

Y_d \ Y_c	*0*	*1*
0	*AllD*	*TFT*
1	*Perv.*	*AllC*

(i) cooperates and (ii) responds to others' cooperation

a *single* random mutation* ?

What if reciprocity was a composite trait?

What if, like most complex functions, reciprocity required *several independent mutations* rather than one?

Reciprocity entails at least *two* novel features:
(i) the ability to cooperate, and
(ii) the ability to detect and respond to others' cooperation

A simple model where reciprocity is a composite trait

individuals are characterized by two traits:

- γ : cooperative tendency « in general »
- ρ : conditional ability

ρ \ γ	*0*	*1*
0	*AllD*	*AllC*
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see also Garćıa and Traulsen (2012)

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A simple model where reciprocity is a composite trait

ρ \ γ	*0*	*1*
0	*AllD*	*AllC*
1	*AllD'*	*TFT*

A simple model where reciprocity is a composite trait

Cooperation is never favored in the absence of reciprocity

ρ \ γ	*0*	*1*
0	*AllD*	*AllC*
1	*AllD'*	*TFT*

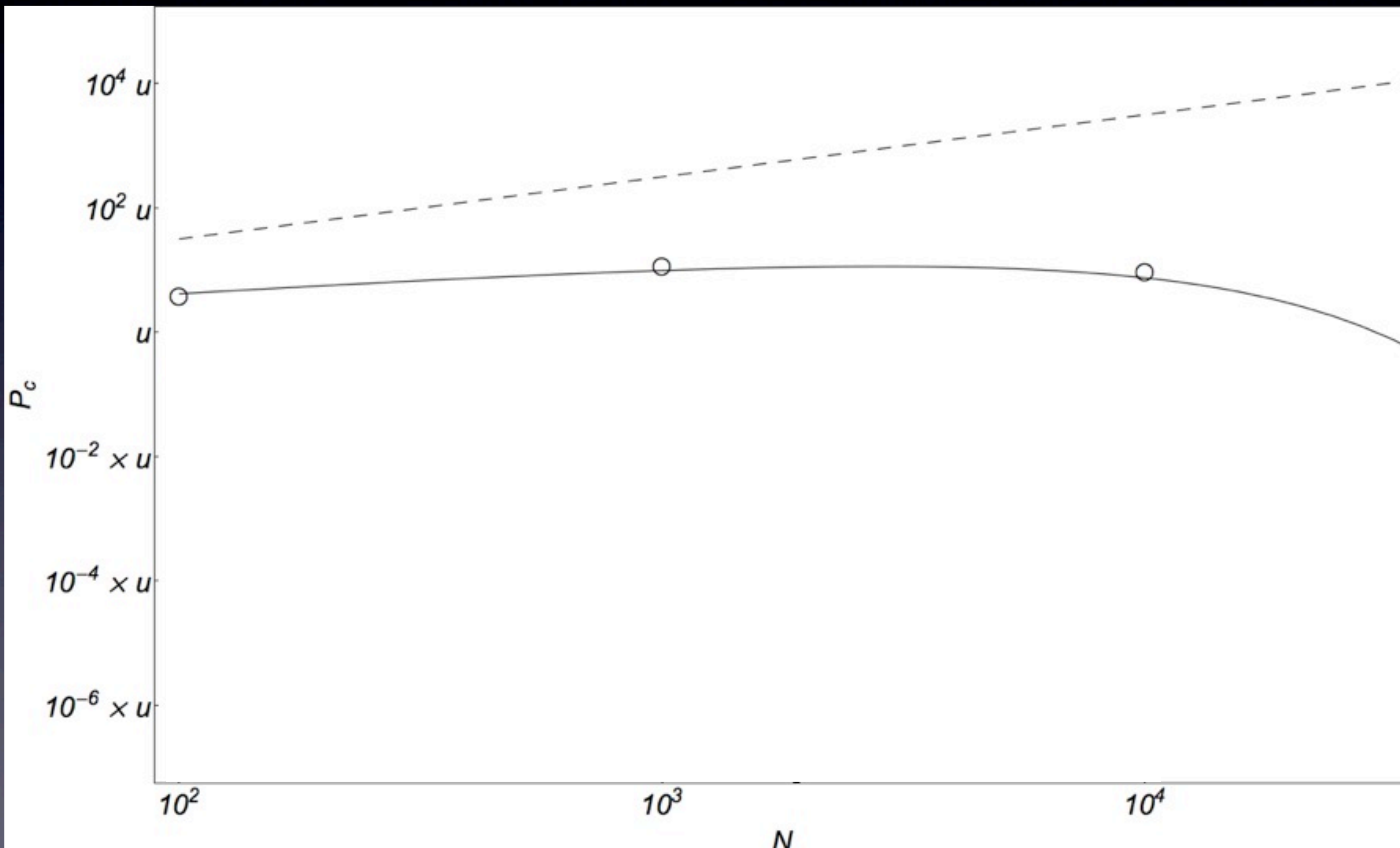
A simple model where reciprocity is a composite trait

Cooperation is never favored in the absence of reciprocity

Conditionality is never favored in the absence of cooperation

ρ \ γ	*0*	*1*
0	*AllD*	*AllC*
1	*AllD'*	*TFT*

Results



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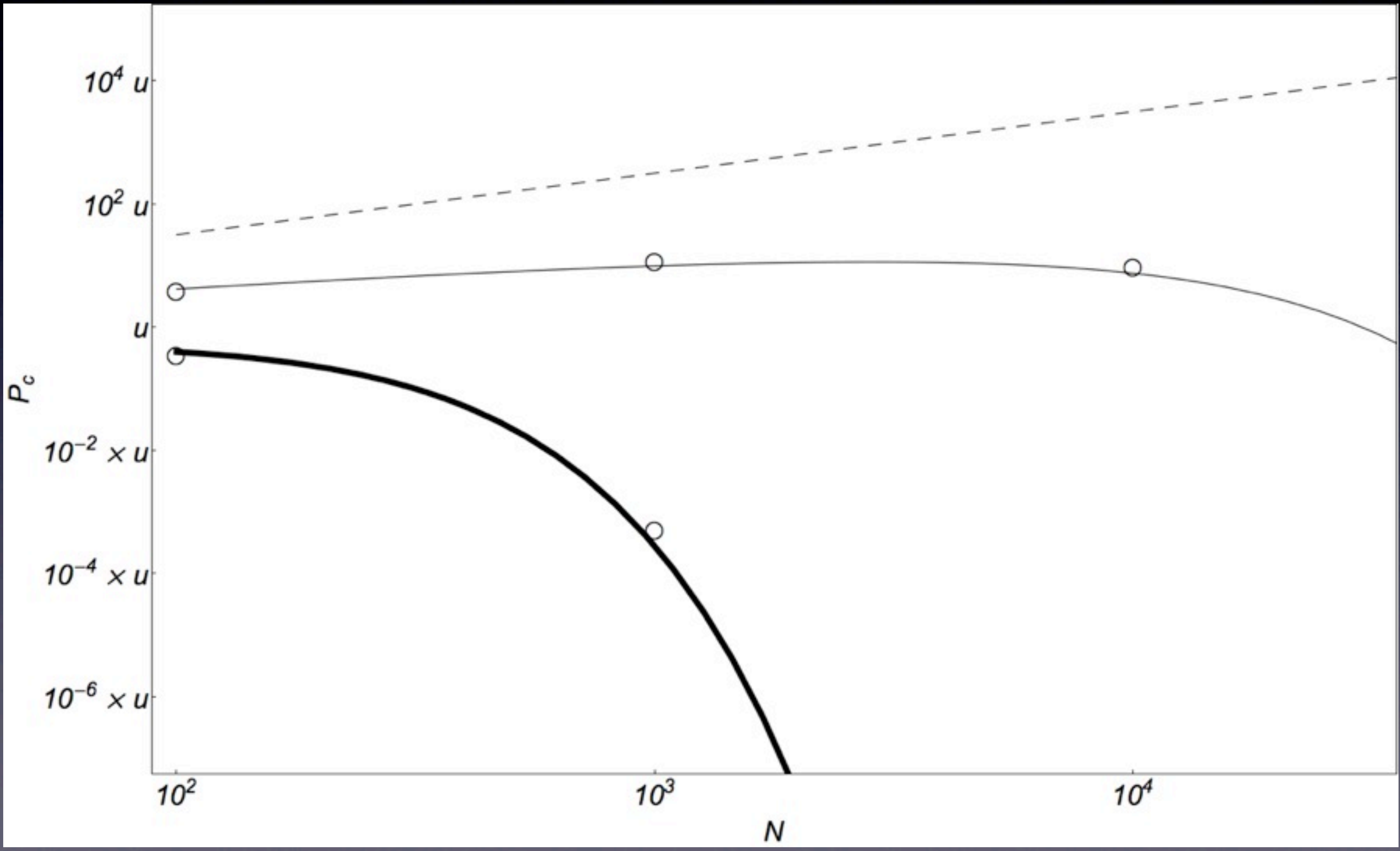
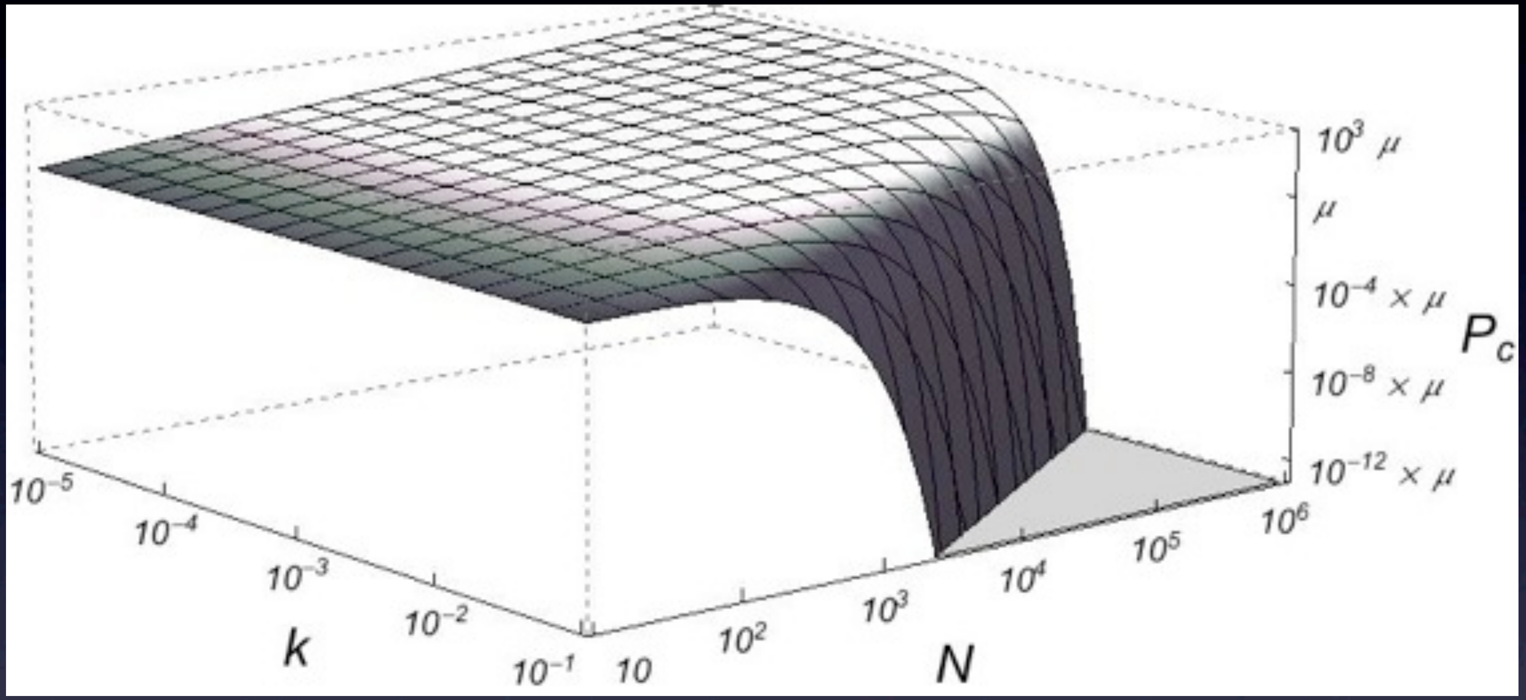
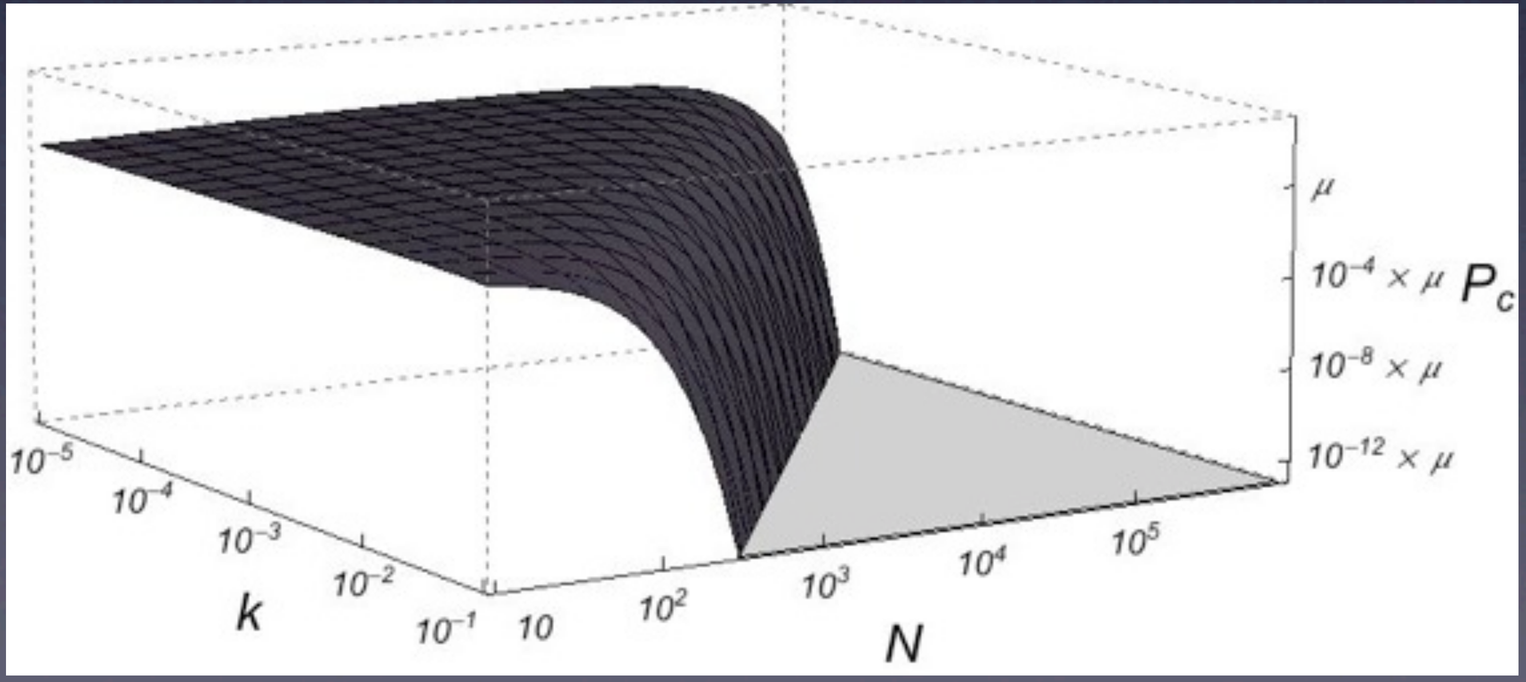


Results

Reciprocity is a simple trait →



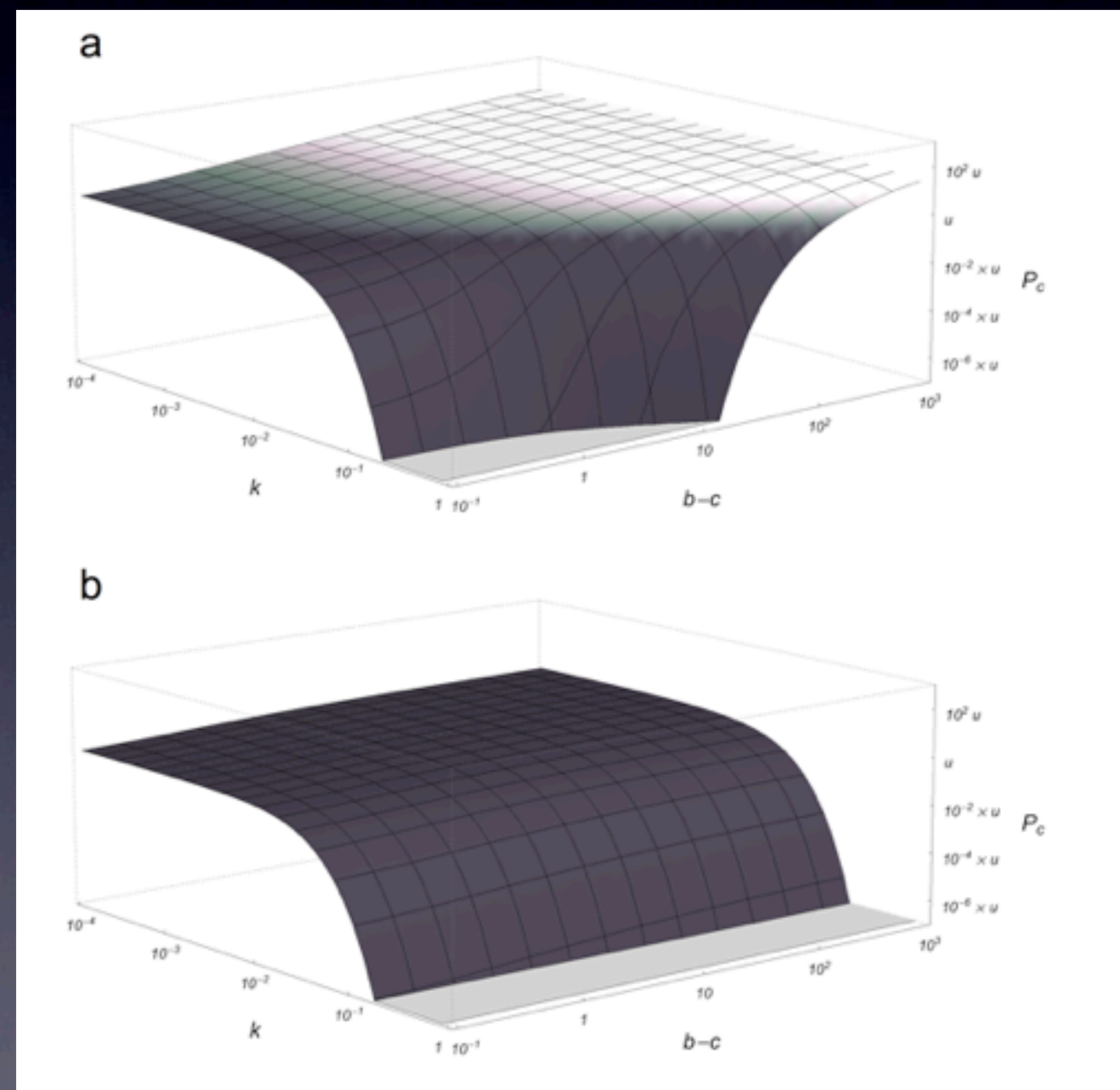
Reciprocity is a composite trait →



The net benefit of cooperation

Reciprocity is a simple trait

Reciprocity is a composite trait

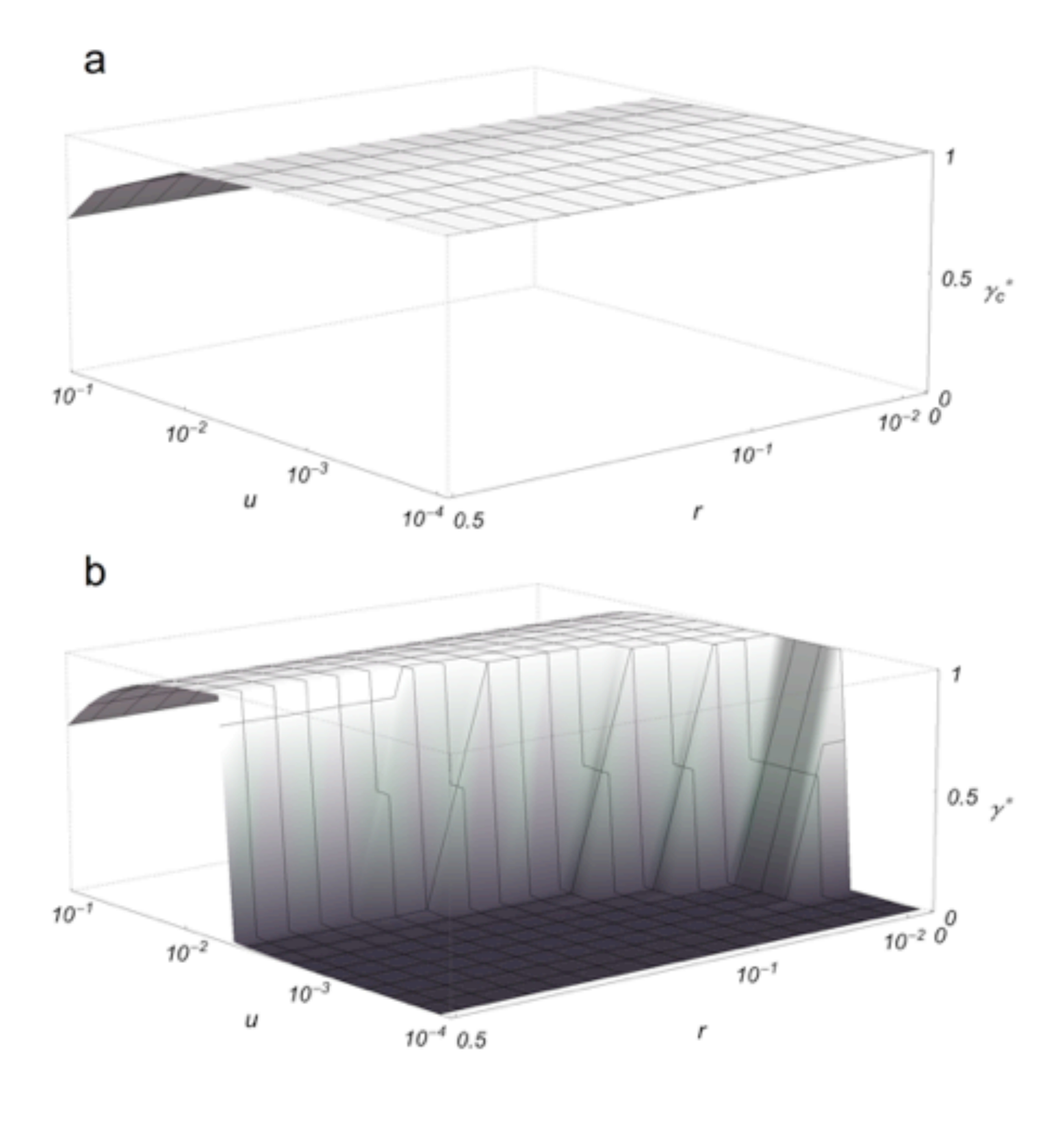


b-c

Recombination

Reciprocity is a simple trait ⟶

Reciprocity is a composite trait ⟶



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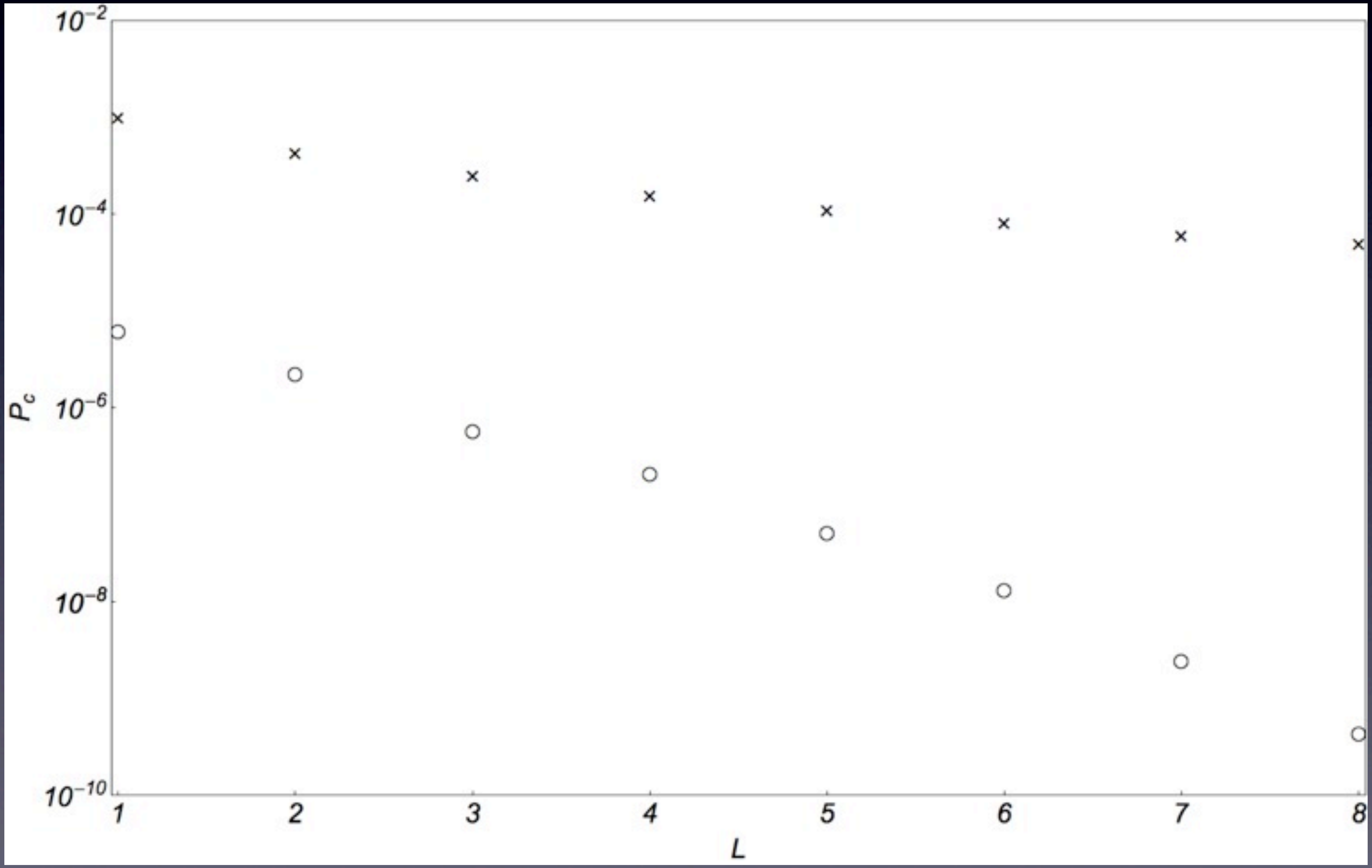
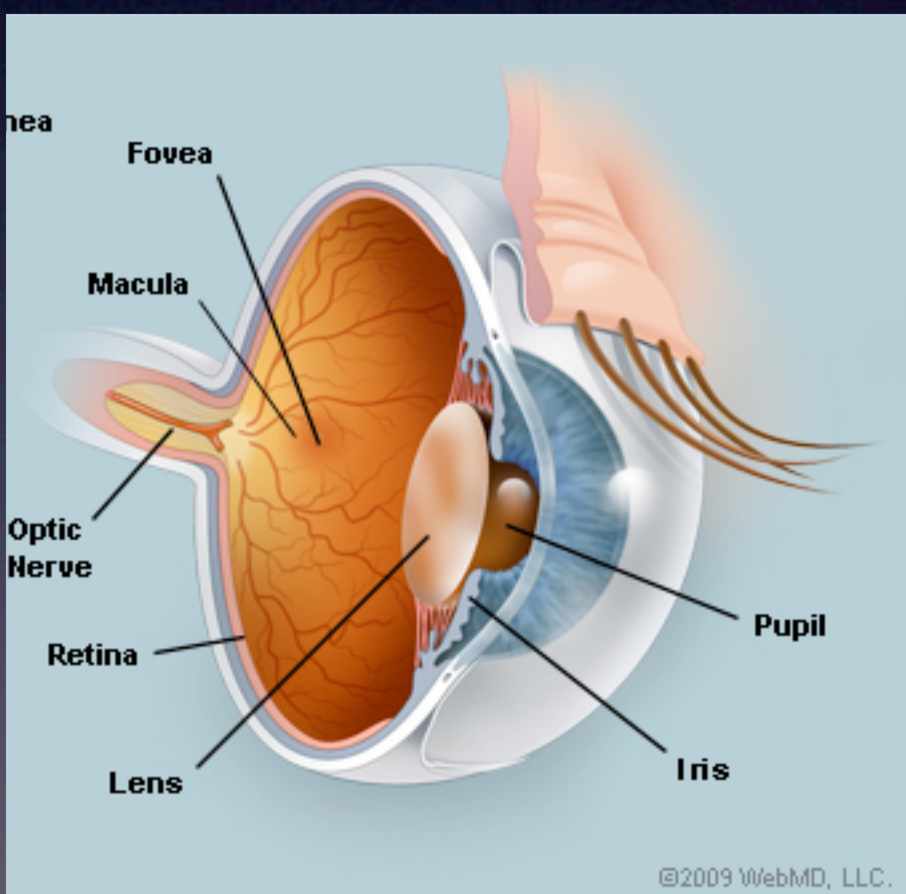
What if reciprocity required more than two mutations?



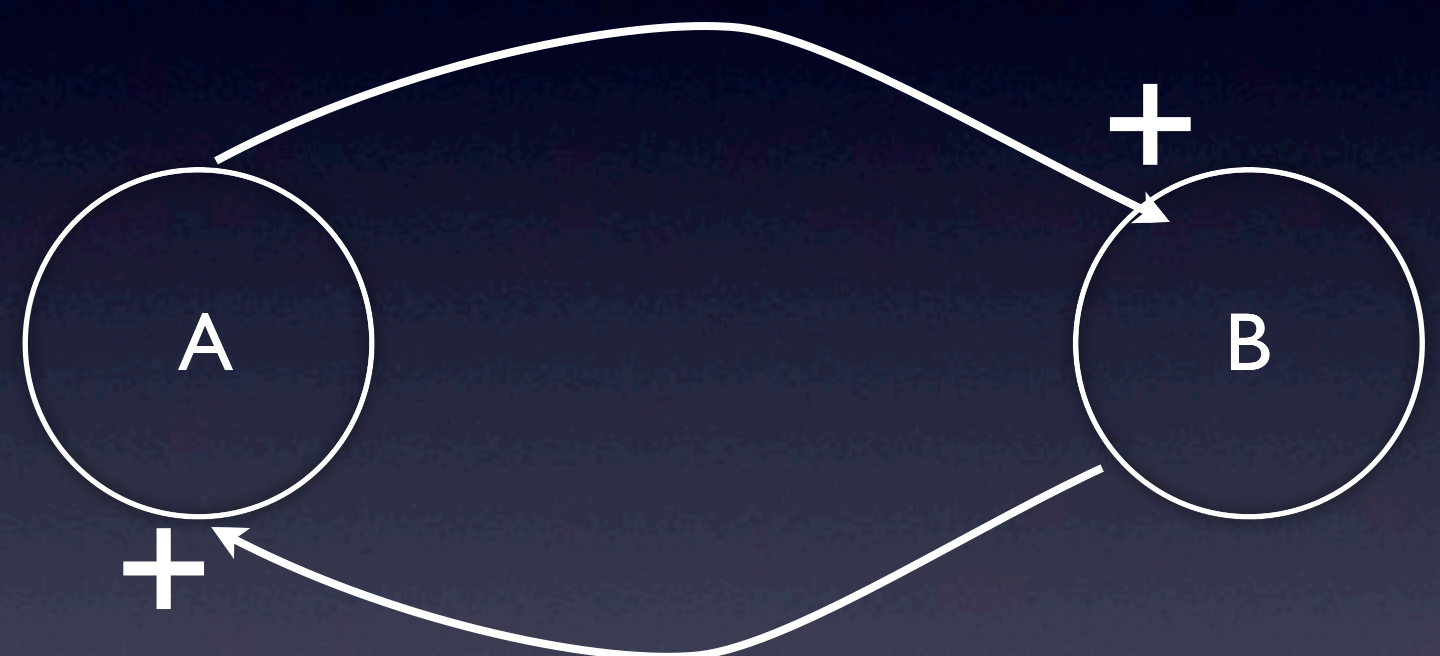
The origin of complex functions



Complex functions are shaped by *directional selection* exherted by the « environment »

Directional selection allows the *accumulation* of adaptive mutations

A problem for reciprocity



Complex functions cannot evolve
when they constitute the very selective pressure
shaping themselves

Conclusion

- If reciprocity is a composite trait,
its evolution by natural selection is extremely unlikely

- The evolution of reciprocity in many models
is a consequence of the facilitating assumption
that a *single* mutation is enough

see also Garćıa and Traulsen (2012)

Three questions

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How has reciprocity evolved?

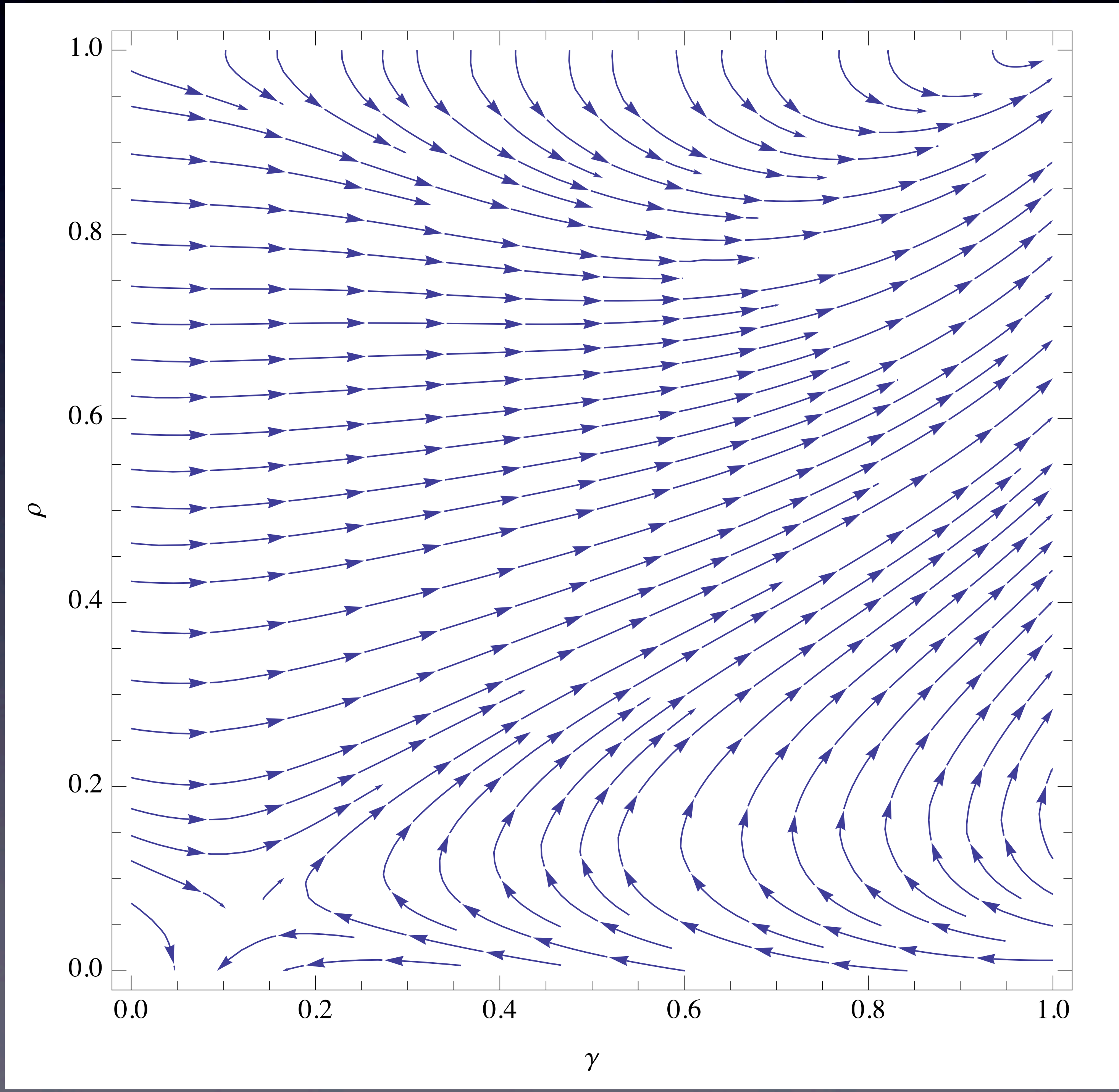
How does evolution solve problems of circularity?

Krebs & Dawkins 1984; Scott-Phillips et al. 2011

Evolutionary recycling

- All the biological functions needed to reciprocate cannot evolve together *at once*
- Some functions needed for reciprocity must evolve before *for a different reason*

Quantitative evolution of cooperation and conditionality



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