

Self-organized assortment and the evolution of collective function

Silvia De Monte
Eco-Evo-Math team, IBENS, Paris



Eco-Evolutionary Dynamics in Nature and in the Lab
KITP, July 28, 2017

Outline

Collective function in microbial collectives
and 'paradox' of evolutionary maintenance of
functional groups

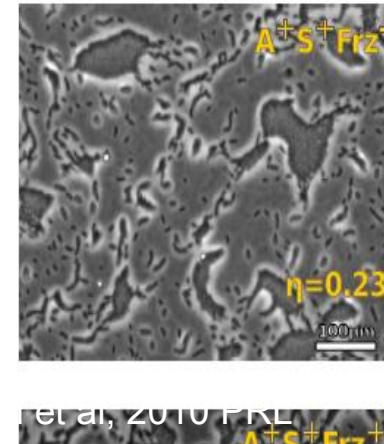
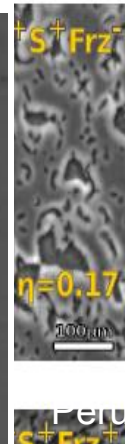
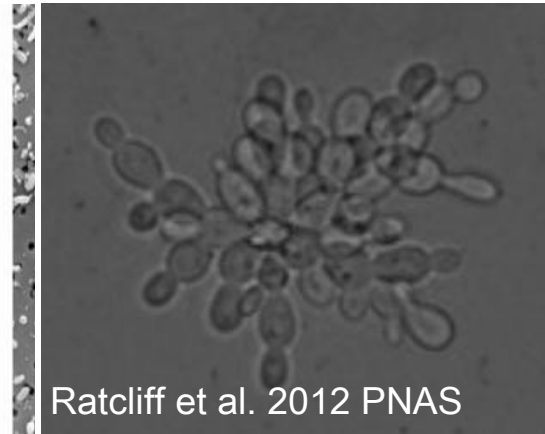
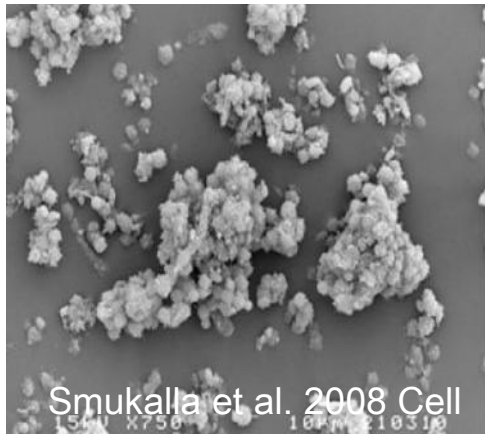
Assortment and ecological dynamics

The adaptive evolution of adhesive groups

Ongoing work

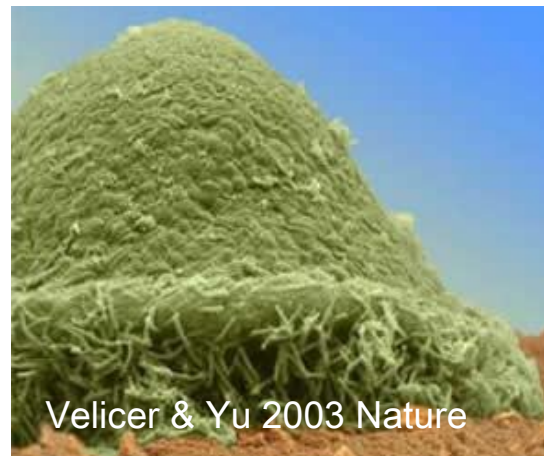
Functional collectives of cells

colonies and
biofilms

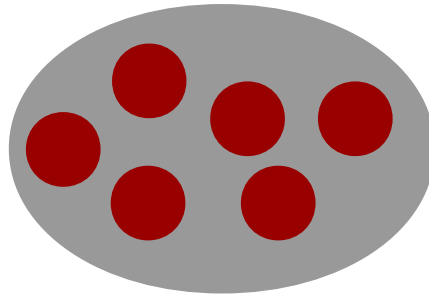


flakes
and
swarms

multicellular
differentiated
fruiting bodies



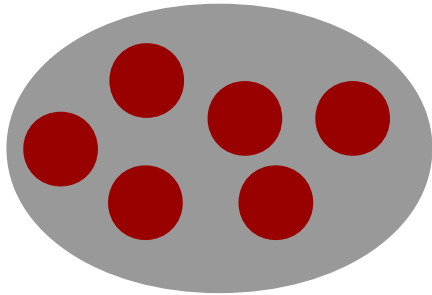
A simplified view of a functional collective



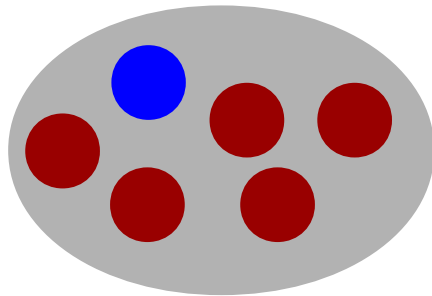
Units: individually dividing cells

Function: Public good

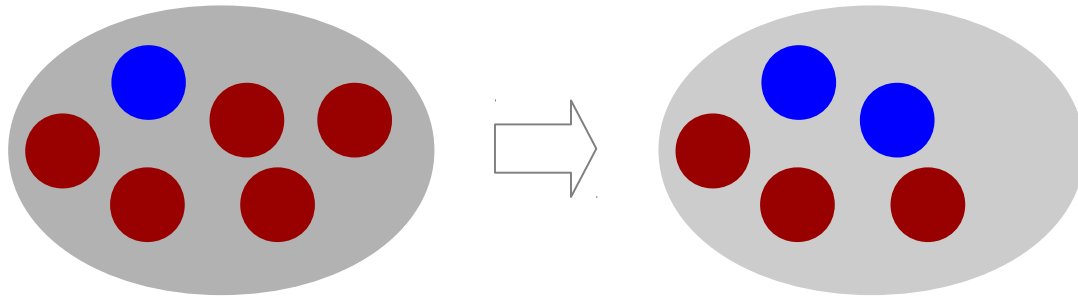
(In) stability of collective function



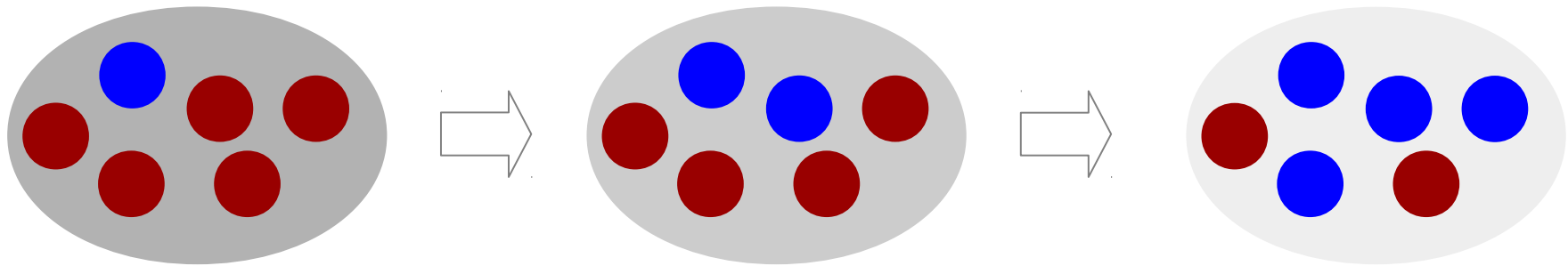
(In) stability of collective function



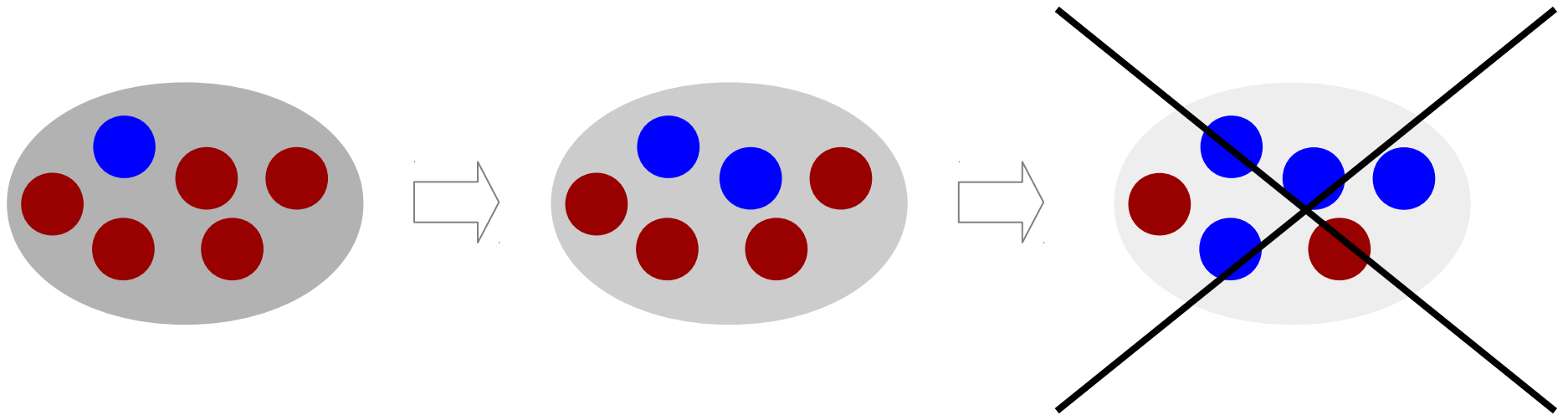
(In) stability of collective function



(In) stability of collective function



(In) stability of collective function



Tragedy of the commons

Hardin, 1968

Rankin et al. TREE 2007

'Paradox' of the evolution and maintenance of collective function

Collective function entails individual costs
and conflicts of interest

Genetic heterogeneity can disrupt function
through within-collective competition

Evolutionary games

Examples:

Prisoner's Dilemma

Public Goods Game

Kin selection

Evolution of cooperation through genetic homogeneity

Hamilton's rule

$$r > \frac{c}{b}$$

Genetic relatedness r : Degree of inbreeding.

Mechanism increasing relatedness: Kinship

Extension: probability of interacting with another individual carrying the allele for cooperation

Mechanism increasing relatedness: Spatial structure

SA West, AS Griffin, A Gardner, SP Diggle
Social evolution theory for microorganisms
Nature Rev Microbiology 2006

Assortment

Average number of cooperators within the interaction group.

JA Flechter and M Doebeli

A simple and general explanation for the evolution of altruism

Proc. R. Soc. B 2009

Assortment is dynamic and ruled by ecology

It accounts for population structure established on the **ecological time scale** of individual interactions

Quantifies the **evolutionary effects** of ecological dynamics

Assortment

Average number of cooperators within the interaction group.

JA Flechter and M Doebeli

A simple and general explanation for the evolution of altruism

Proc. R. Soc. B 2009

Assortment is dynamic and ruled by ecology

It accounts for population structure established on the **ecological time scale** of individual interactions

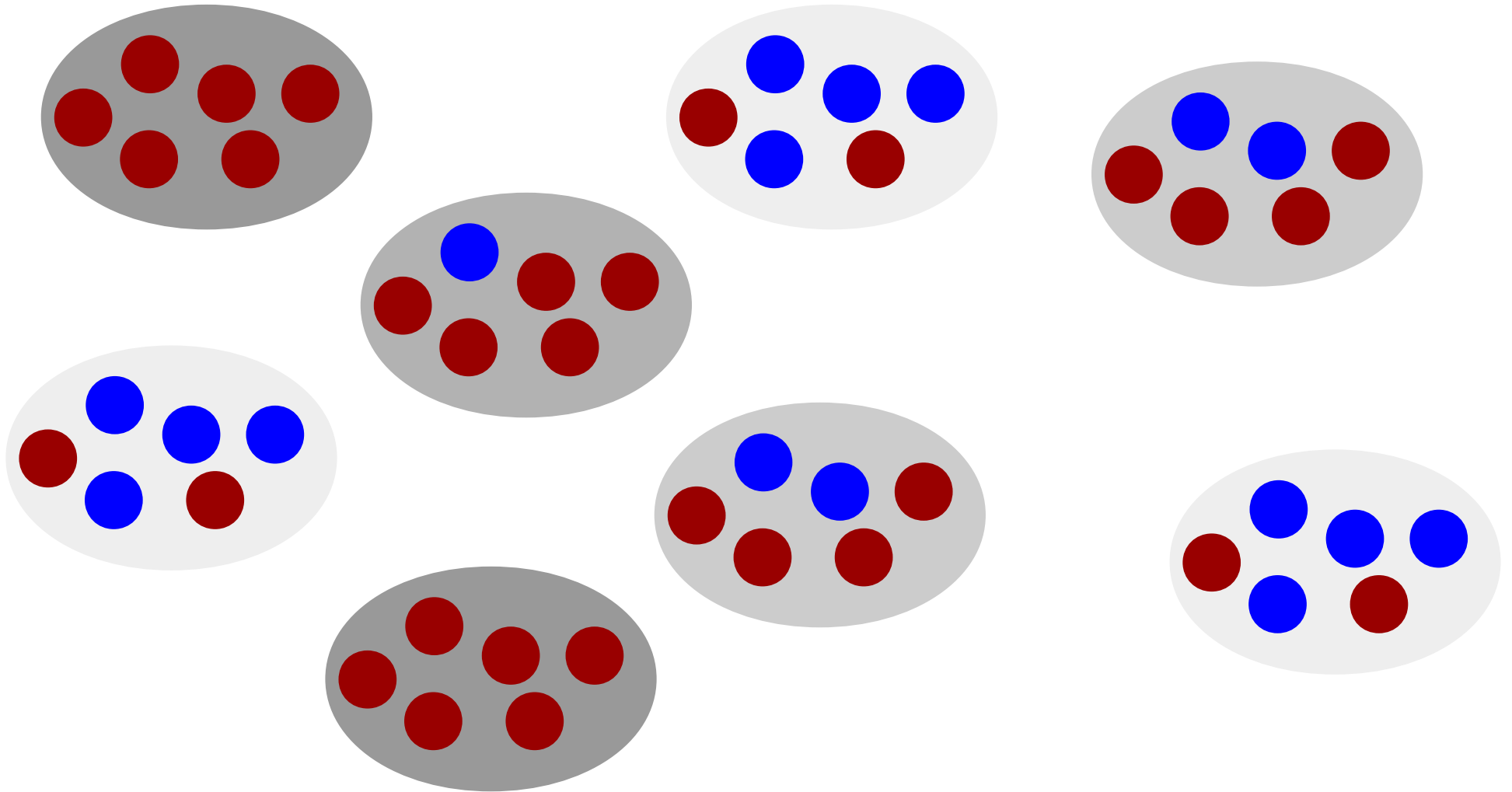
Quantifies the **evolutionary effects** of ecological dynamics

Difference between within-group fitness and population-level (weighted) averages

Chuang, Rivoire, Leibler (2009) Science

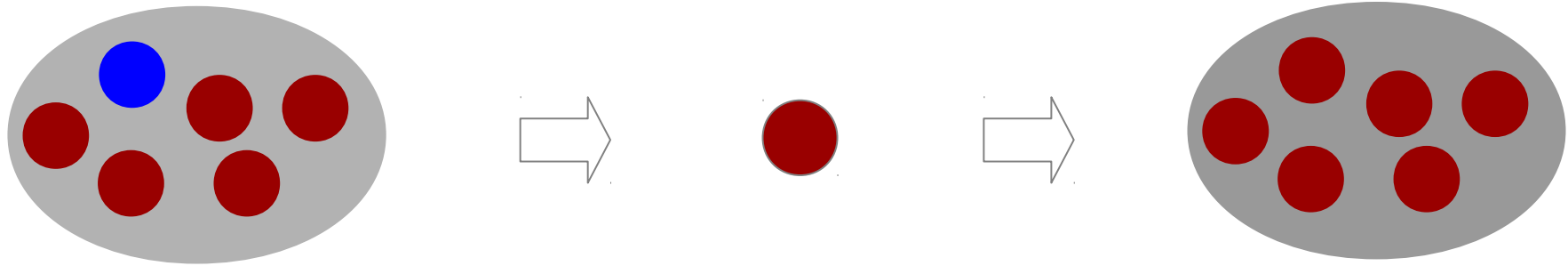
Simpson's paradox in a synthetic microbial system

A population of recurrent groups



How does assortment change when groups recur (life cycle)?

Life cycles & heredity of function



'staying together' type

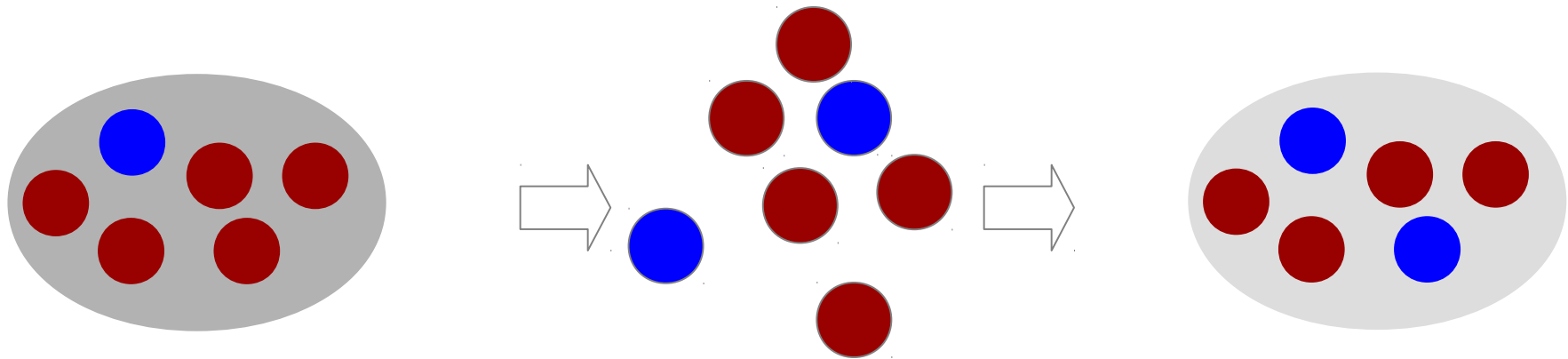
Efficient purging of non-contributors
low levels of intra-group conflict
but strong competition for resources

Tarnita C. et al. (2013) JTB

Rainey P.B. and De Monte S. (2014), Ann. Rev. Ecol. and Syst.

De Monte S. and Rainey P.B. (2014) J. Biosciences

Life cycles & heredity of function



'coming together' type

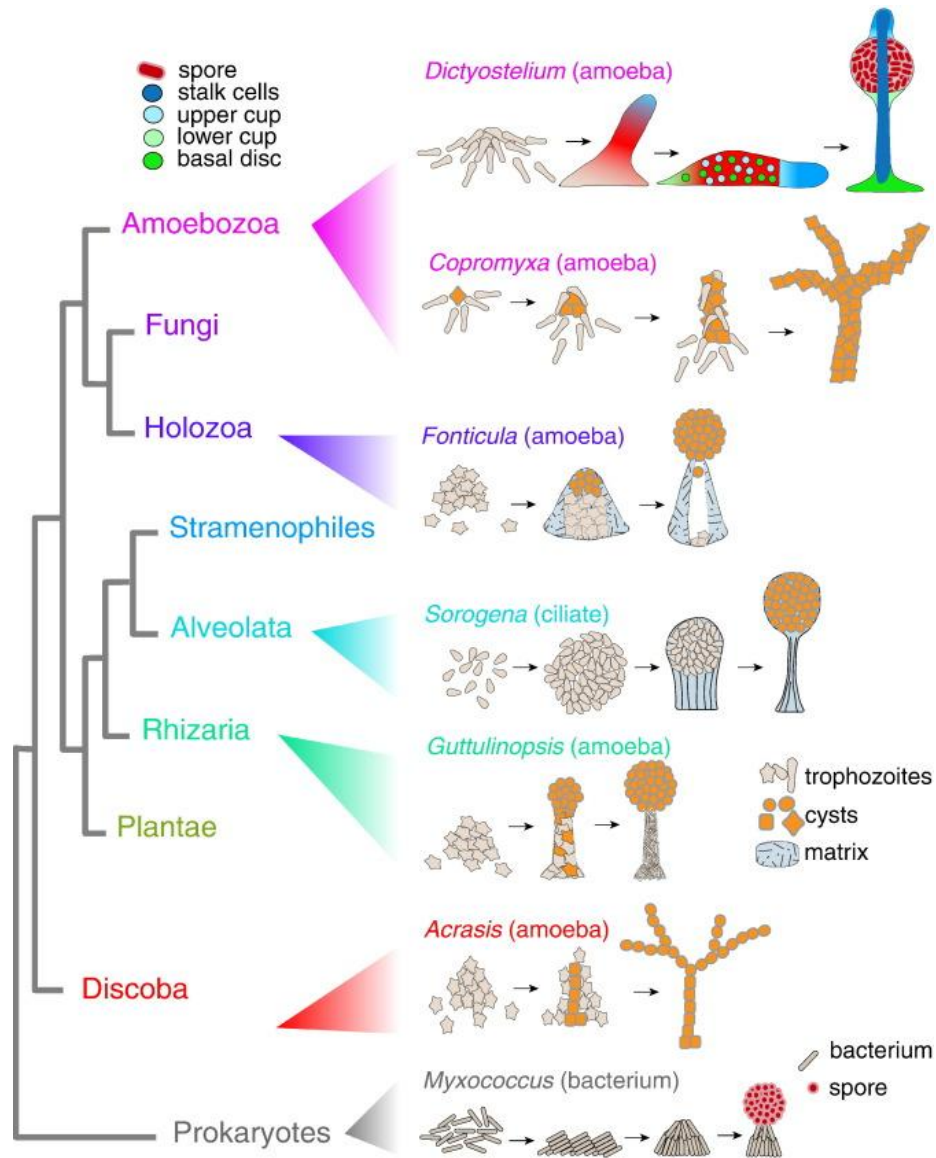
(potentially) genetically heterogeneous
high levels of intra-group conflict

Tarnita C. et al. (2013) JTB

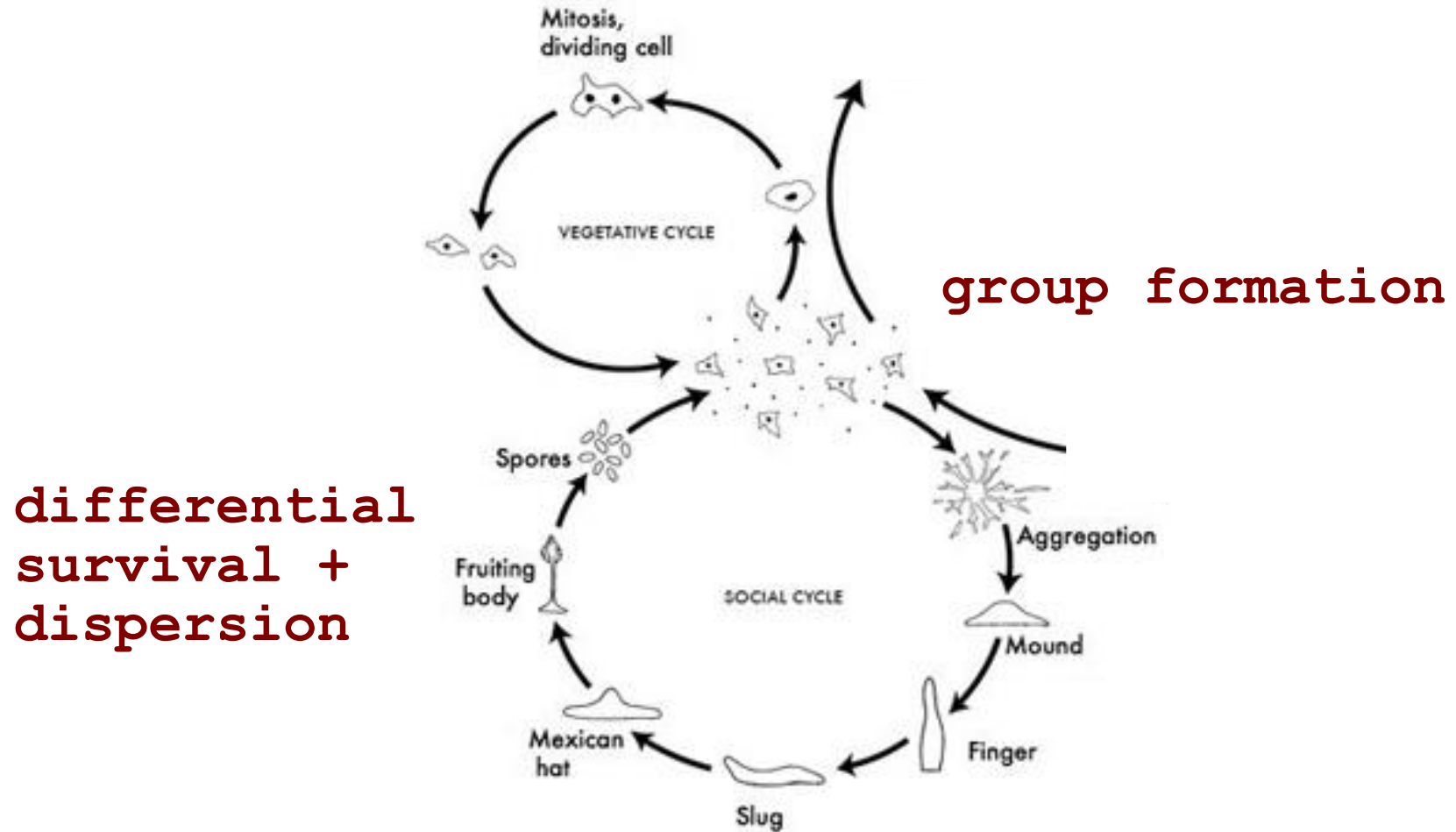
Rainey P.B. and De Monte S. (2014), Ann. Rev. Ecol. and Syst.

De Monte S. and Rainey P.B. (2014) J. Biosciences

Aggregative multicellularity



The 'social' amoeba *Dictyostelium discoideum*



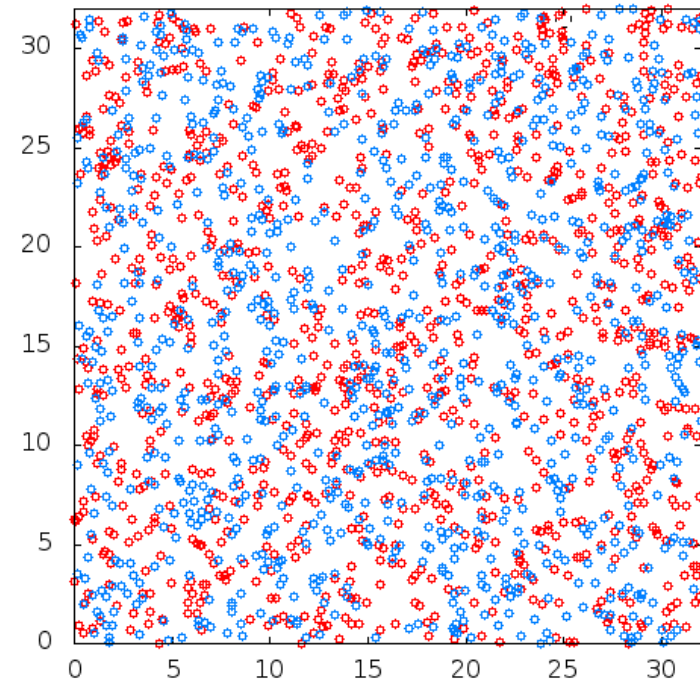
Dictyostelium discoideum



Sandrine Adiba, Charles Bernard

Modeling emergent population structure

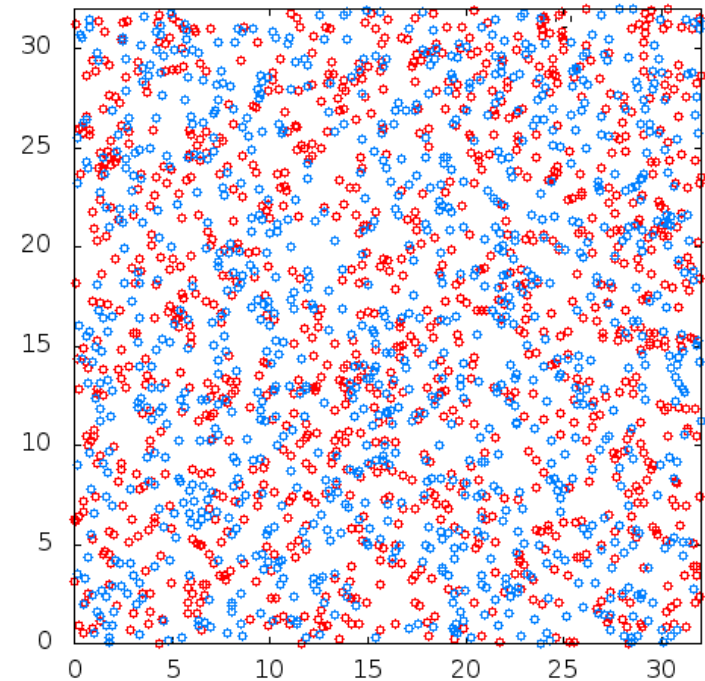
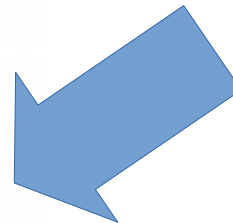
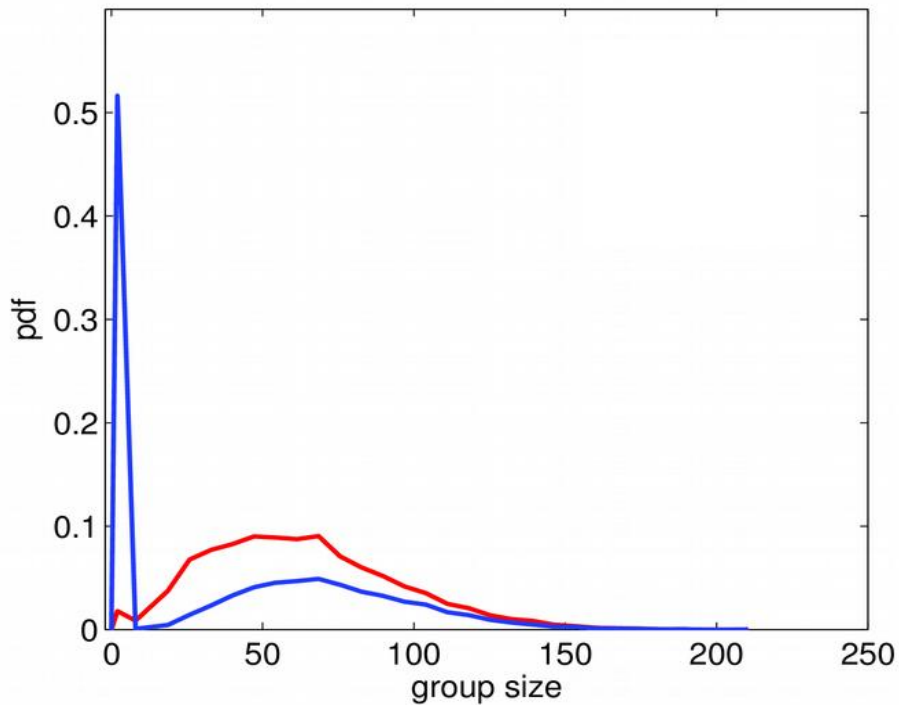
group formation



Garcia T., Gregory-Brunnet L.
and SDM (2014) PLoS Comp. Biol.

Modeling emergent population structure

group formation



Garcia T., Gregory-Brunnet L.
and SDM (2014) PLoS Comp. Biol.

Group size distributions \Rightarrow **differential survival**

u proportion of cells that do not belong to any group
 $g(n)$ proportion of cells belonging to groups of size n

Interactions through adhesion

Adhesiveness: trait underpinning cell interaction

➔ costly

➔ effects on group formation as well as group-related benefits

Development 138, 2487-2497 (2011) doi:10.1242/dev.060129
© 2011. Published by The Company of Biologists Ltd

The cell adhesion molecule DdCAD-1 regulates morphogenesis through differential spatiotemporal expression in *Dictyostelium discoideum*

Shrivani Sriskanthadevan, Yingyue Zhu, Kumararaj Manoharan, Chunxia Yang and Chi-Hung Siu*

Proc. Natl. Acad. Sci. USA
Vol. 95, pp. 12376–12380, October 1998
Evolution

Loss of social behaviors by *Myxococcus xanthus* during evolution in an unstructured habitat

GREGORY J. VELICER*†‡, LEE KROOS*, AND RICHARD E. LENSKI†

Adaptive dynamics of adhesiveness

z quantitative trait measuring interaction strength upon cell contact

Thomas Garcia, Guilhem Doulcier

Adaptive dynamics of adhesiveness

z quantitative trait measuring interaction strength upon cell contact

Mutation-substitution evolutionary process:

\hat{z} trait of a resident, monomorphic population

z trait of a mutant

If the fitness of the mutant is larger than that of the resident, the mutant substitutes the resident.

Odo Diekmann

A beginner's guide to Adaptive Dynamics

Adaptive dynamics of adhesiveness

z quantitative trait measuring interaction strength upon cell contact

Mutation-substitution evolutionary process:

\hat{z} trait of a resident, monomorphic population

z trait of a mutant

If the fitness of the mutant is larger than that of the resident, the mutant substitutes the resident.

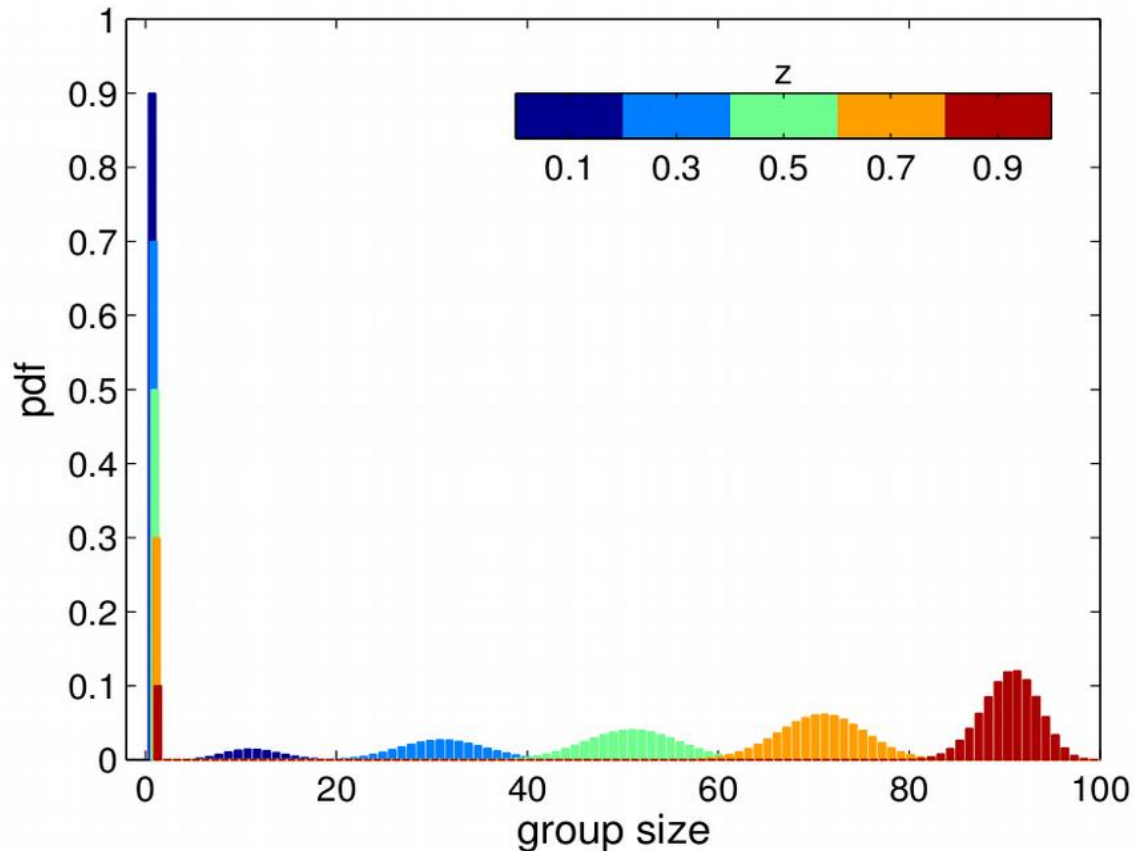
In order to compute fitness, one has to know the population (grouping) structure, thus the ecological dynamics

Ecological time scale:

1. Self-organized population structure

Group size distribution after aggregation

$u(z)$ proportion of cells that do not belong to any group
 $g(n, z)$ proportion of cells belonging to groups of size n



Group formation based on random sequential interactions within patches of size $T=100$

T. Garcia & SDM
Evolution (2013)

Evolutionary time scale:

2. Reproduction

Collective performance depends on the average adhesiveness Z within a group

Fitness of a z cell in a group of average Z

$$bZ - cz$$

b benefit from group coherence

c cost of glue production

Evolutionary time scale:

2. Reproduction

Collective performance depends on the average adhesiveness Z within a group

Fitness of a z cell in a group of average Z

$$bZ - cz$$

b benefit from group coherence

c cost of glue production

'Social dilemma'

Fitness increases with average group adhesiveness

Fitness decreases with individual adhesiveness

Evolutionary time scale:

2.Reproduction

Collective performance depends on the average adhesiveness Z within a group

Fitness of a z cell in a group of average Z

$$b Z - c z$$

b benefit from group coherence

c cost of glue production

Dispersion in a well-mixed population before the following aggregation

Adaptive dynamics of adhesiveness

Will a more adhesive mutant \hat{z} invade the z resident population?

Selection gradient (change in marginal gains upon increase in z)

$$\left. \frac{\partial S(z, \hat{z})}{\partial z} \right|_{z=\hat{z}} = b \hat{z} h(\hat{z}) + b \sum_{n \geq 2} \frac{1}{n} g(n, \hat{z}, \hat{z}) - c,$$

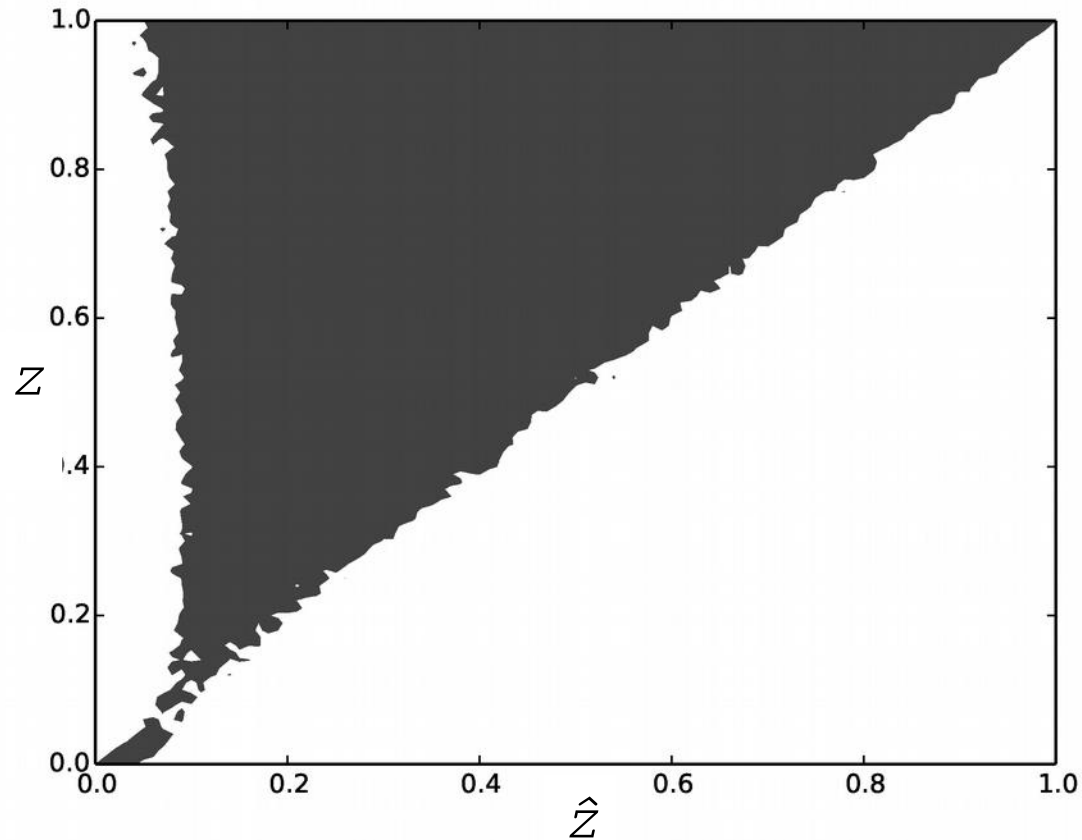
$$h(\hat{z}) = - \left. \frac{\partial u(z, \hat{z})}{\partial z} \right|_{z=\hat{z}}$$

Invasion success depends on:

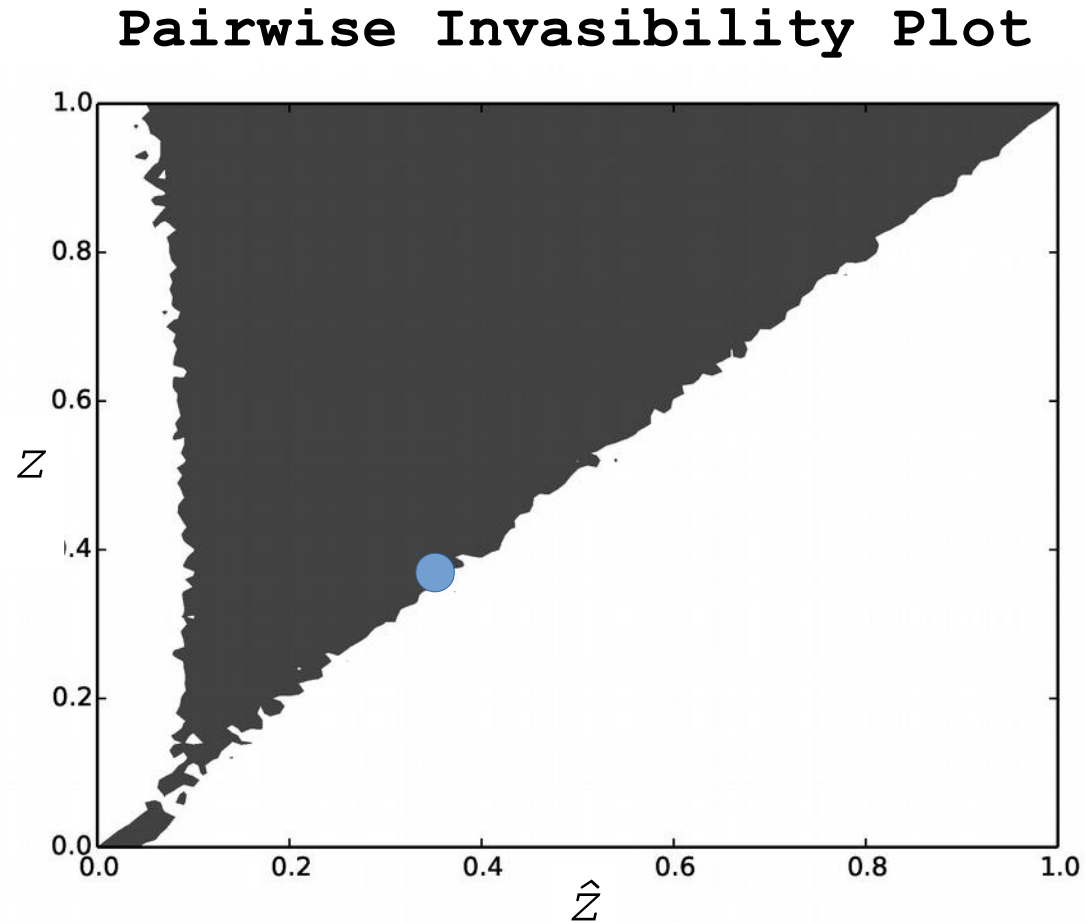
- Collective function and repartition into groups
- Effect of adhesiveness on the proportion of ungrouped cells

The adaptive evolution of groups

Pairwise Invasibility Plot

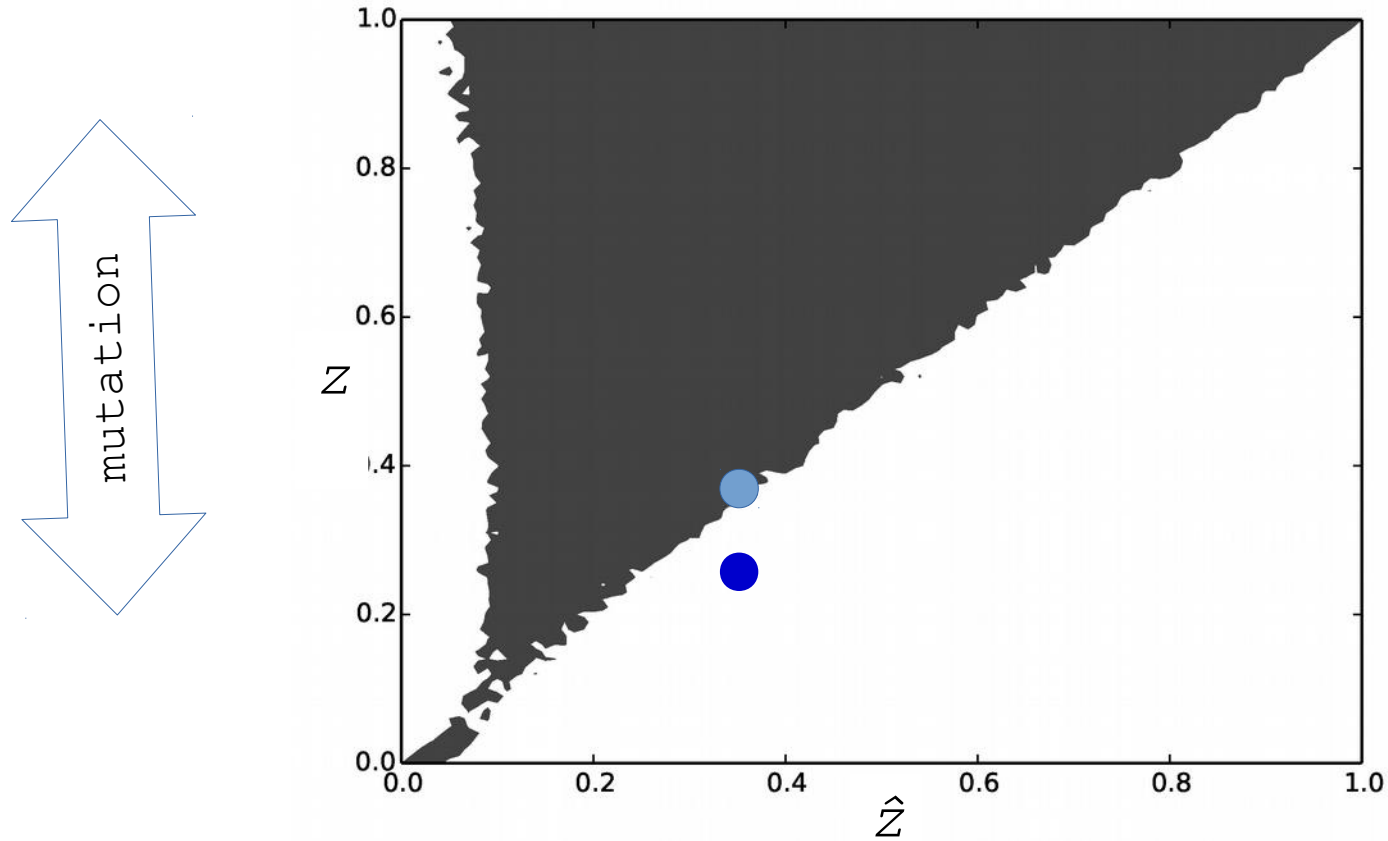


The adaptive evolution of groups

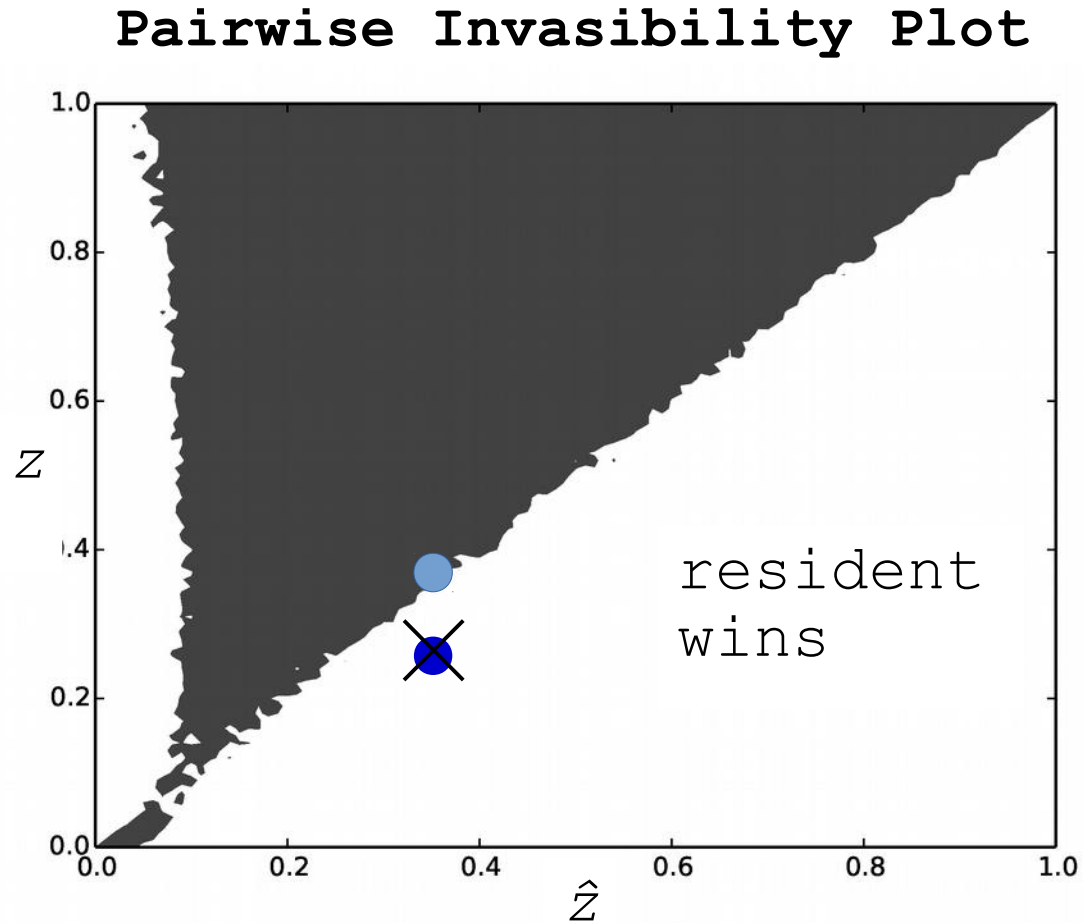


The adaptive evolution of groups

Pairwise Invasibility Plot

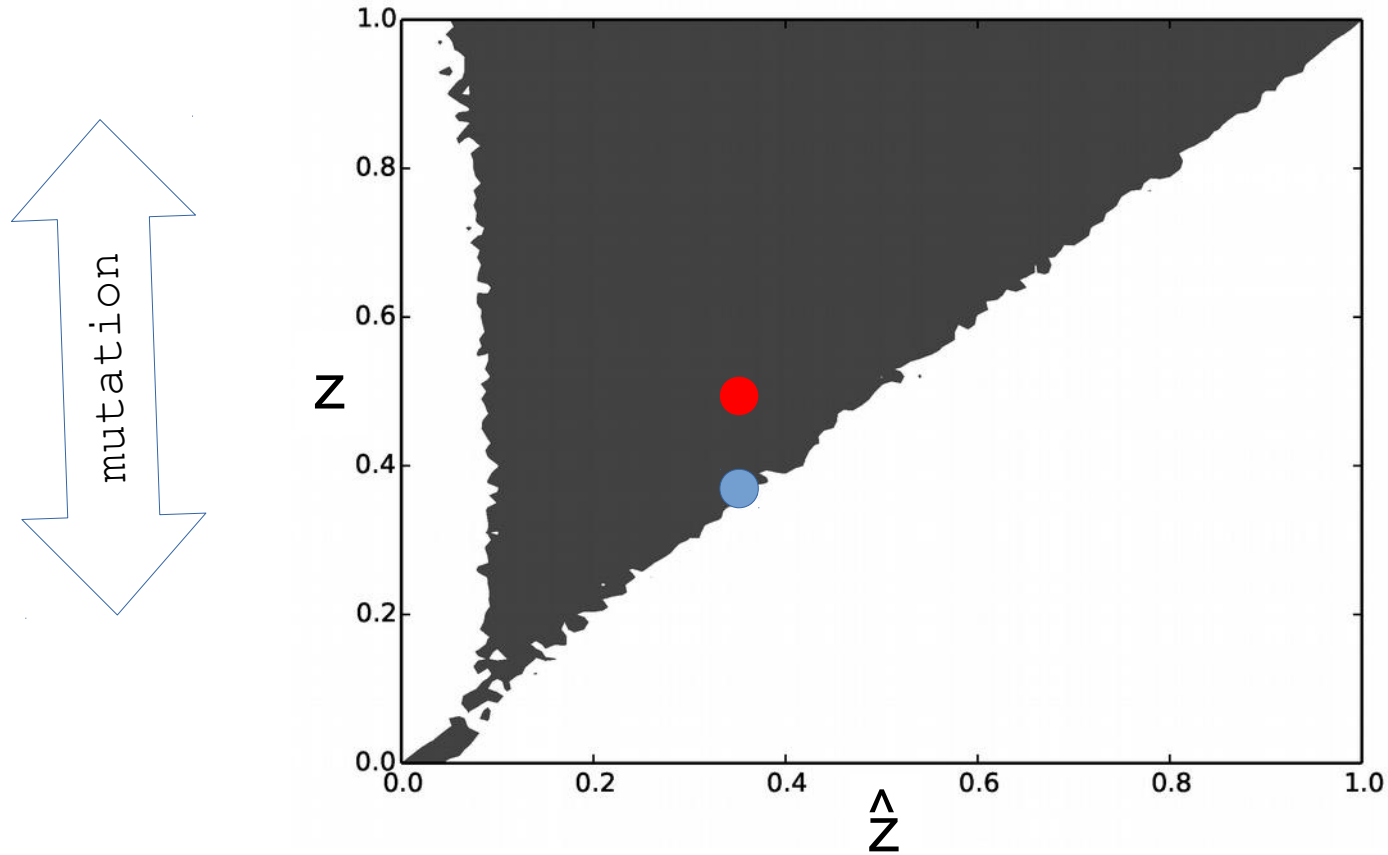


The adaptive evolution of groups

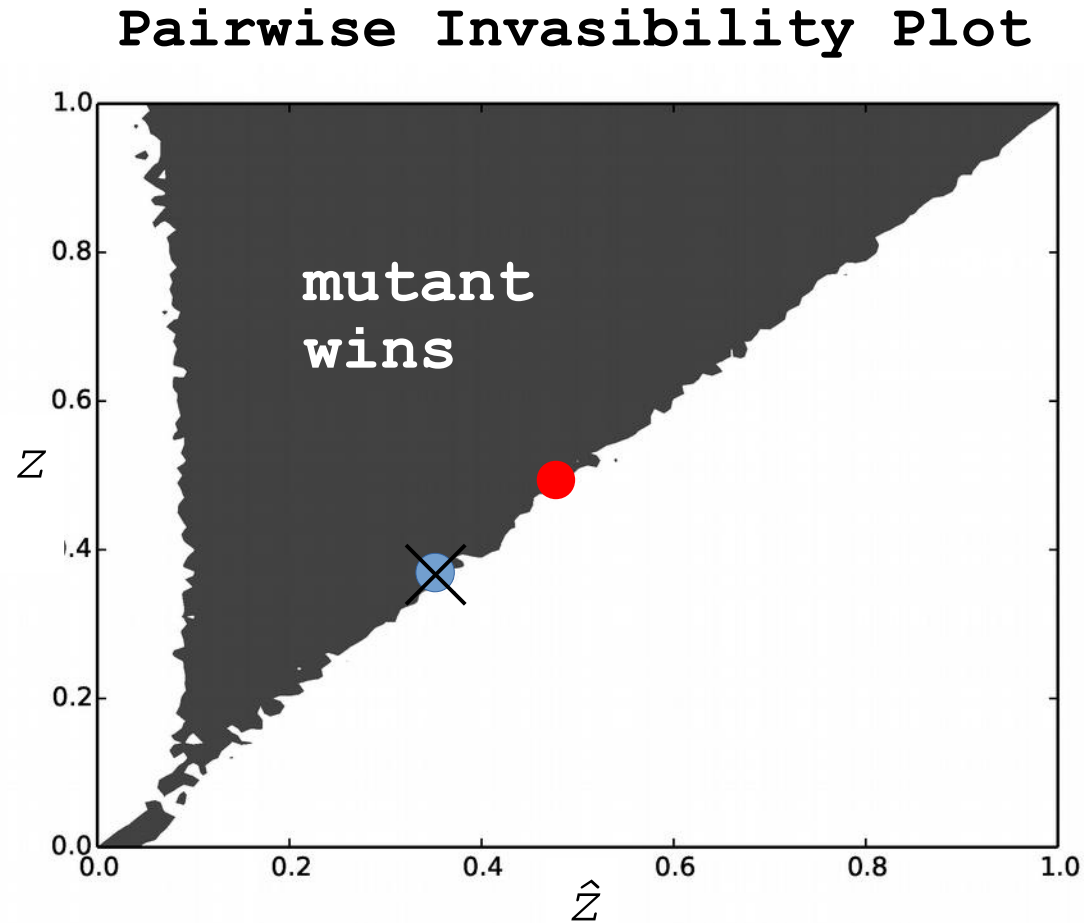


The adaptive evolution of groups

Pairwise Invasibility Plot

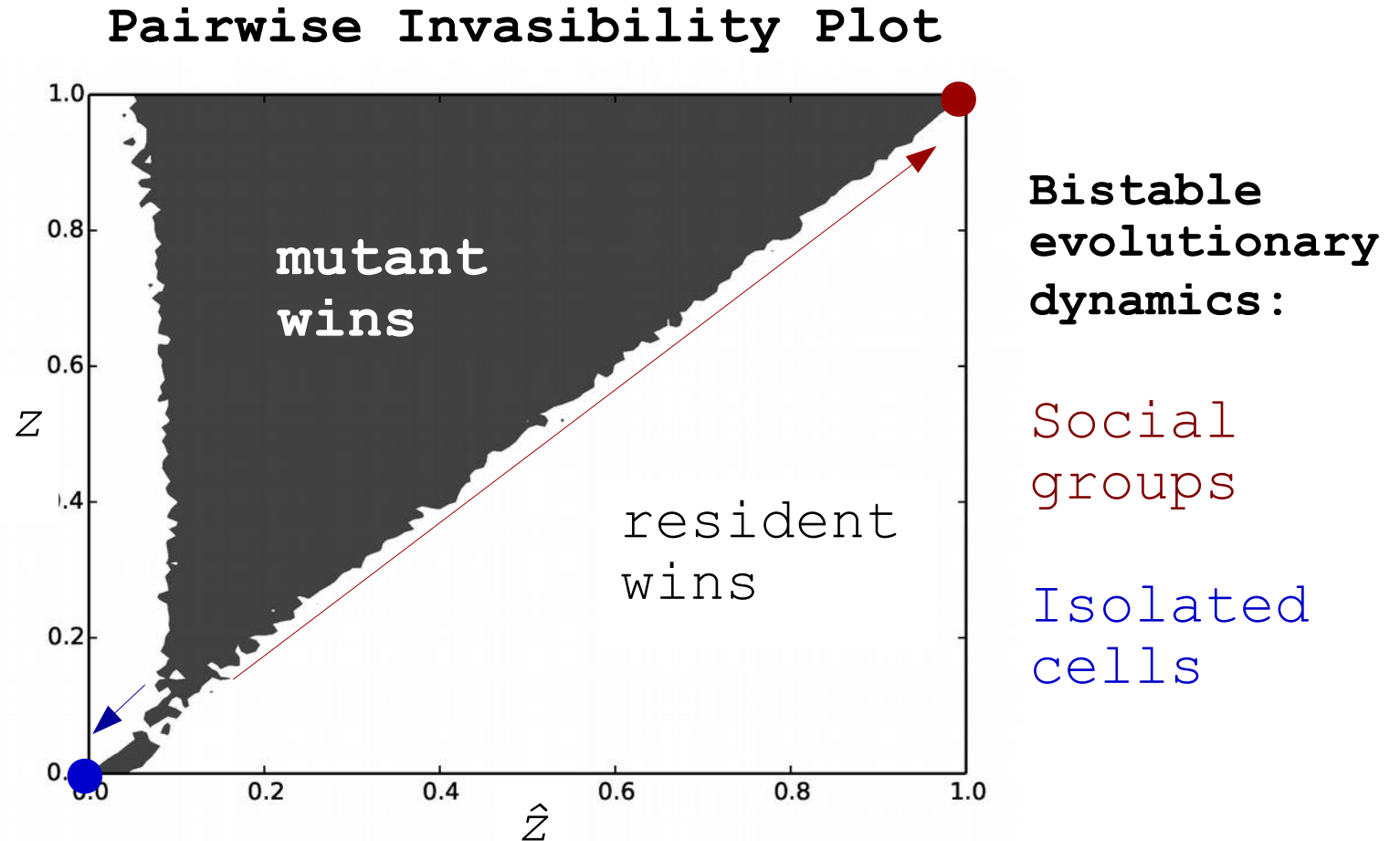


The adaptive evolution of groups



substitution

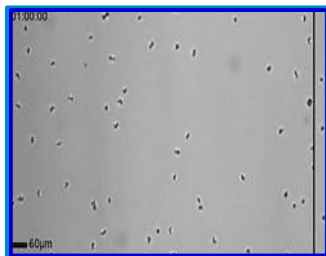
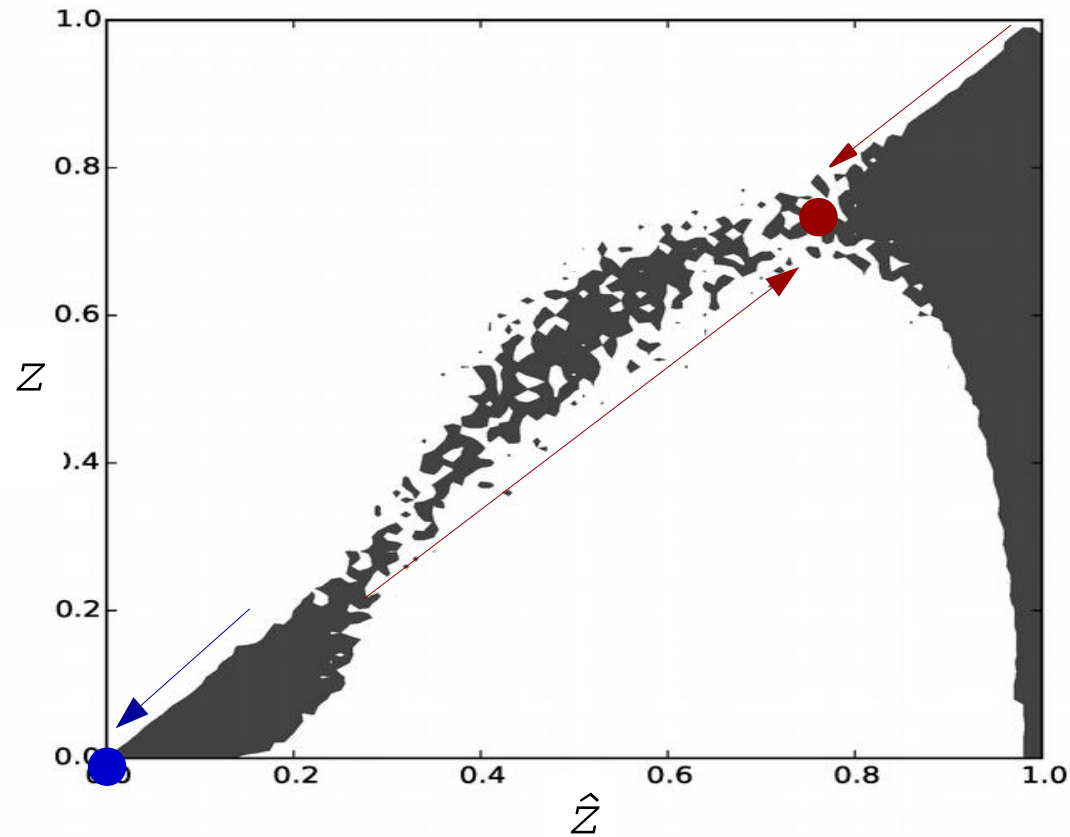
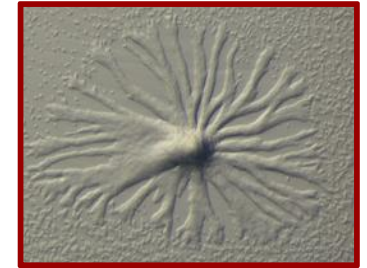
The adaptive evolution of groups



More adhesive mutants exploit the population structure established by the resident.

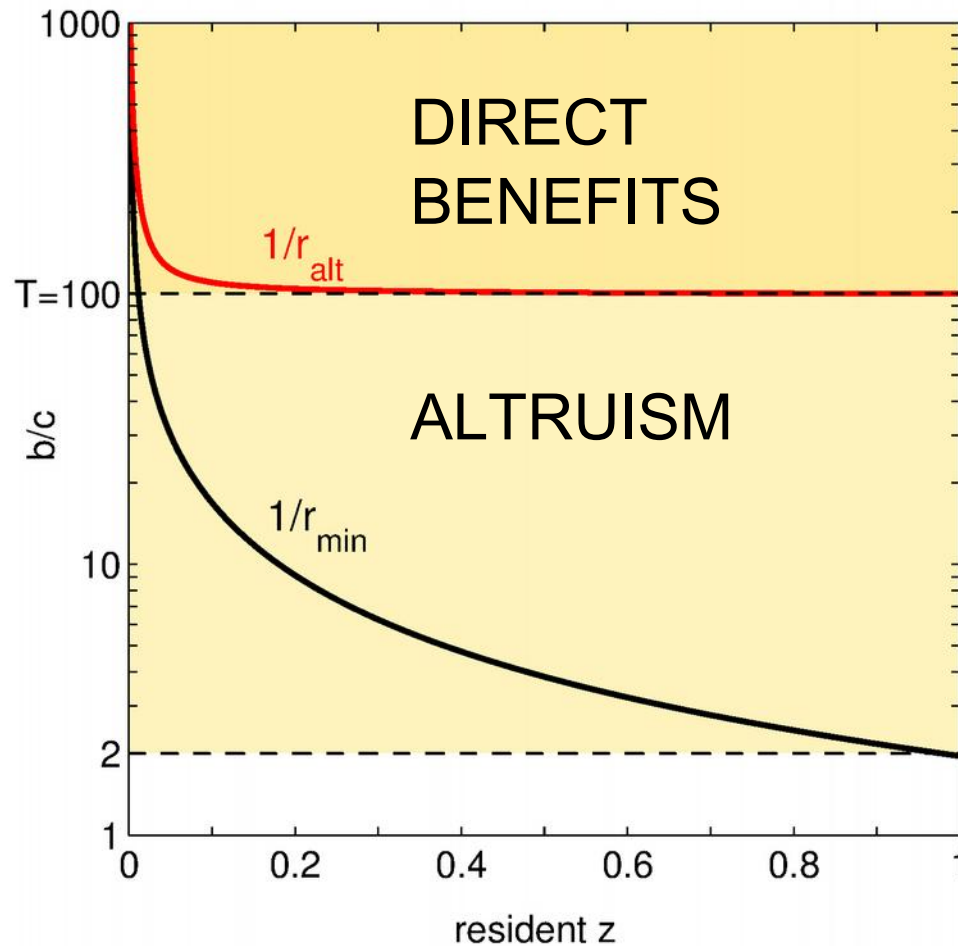
The adaptive evolution of groups

Nonlinear costs



Social groups can coexist with isolated cells at the evolutionary equilibrium.

On the 'social' nature of mutations



More adhesive mutations are initially always 'altruistic'
Later on, they can become directly beneficial

Conclusions

When the costly trait concurring to the collective function also affects assortment (through group formation), groups with a collective function evolve from scratch in an aggregation-dispersal life cycle

Minimal assumptions: no kinship, recognition, punishment, etc.

Co-evolution of population structure and collective function allows ratcheting up costly investments

Even particles that are not in groups have a part in the evolution of collective function

The most boring of functional outcomes: groups of identical units that manage to survive

Ongoing work

1. Eco-evolutionary role of solitary cell

An evolutionarily significant unicellular strategy in response to starvation stress in *Dictyostelium* social amoebae

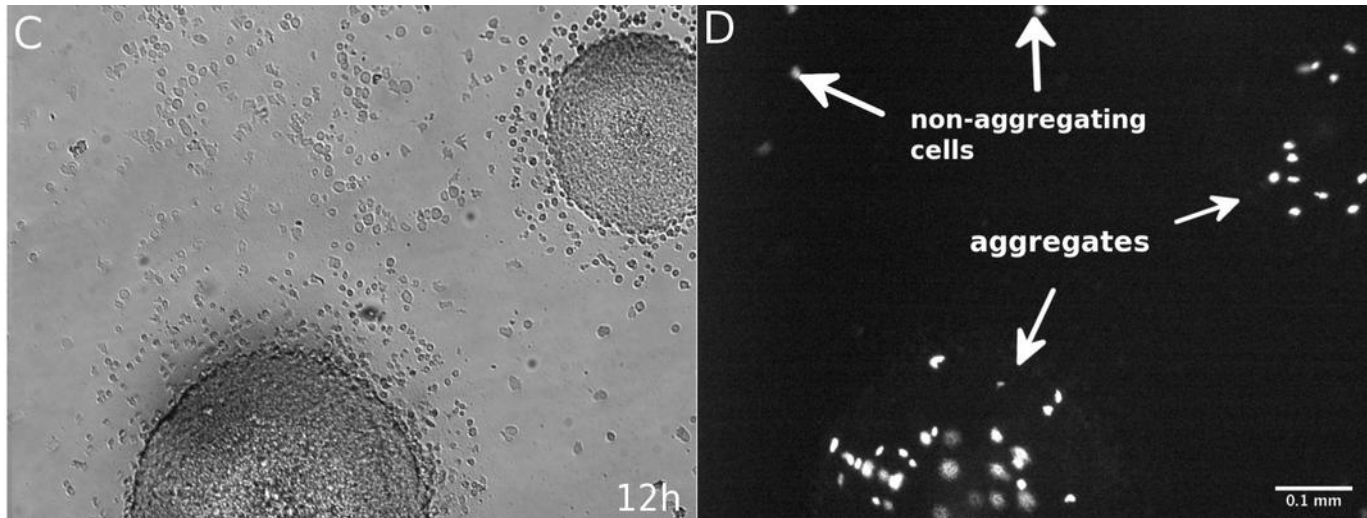
Darja Dubravcic^{1,2}, Minus van Baalen², Clément Nizak^{1,3}

F1000Research 2014, 3:133

Fitness tradeoffs between spores and nonaggregating cells can explain the coexistence of diverse genotypes in cellular slime molds

Corina E. Tarnita^{a,1,2}, Alex Washburne^{a,b,1}, Ricardo Martinez-Garcia^a, Allison E. Sgro^{b,c}, and Simon A. Levin^{a,2}

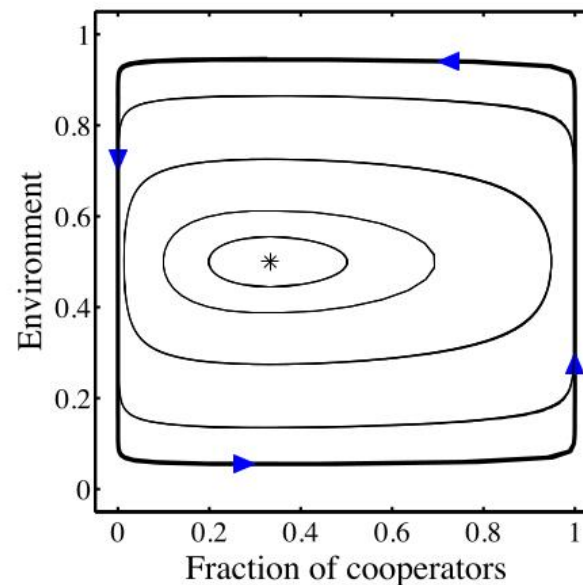
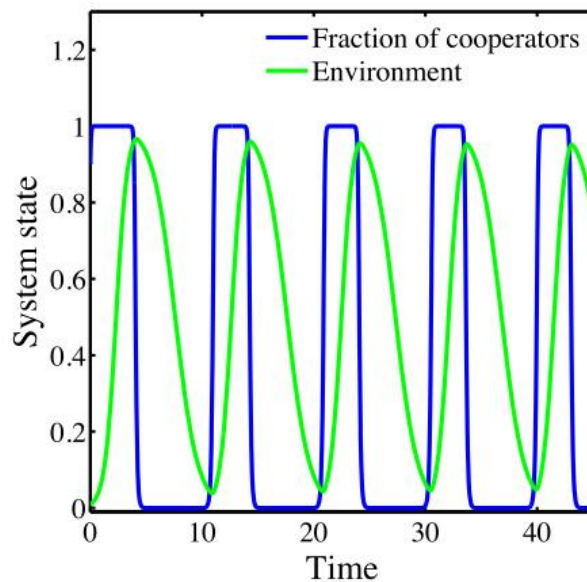
2776–2781 | PNAS | March 3, 2015 | vol. 112 | no. 9



Ongoing work

1. Eco-evolutionary role of solitary cell

$$\begin{aligned}\epsilon \dot{x} &= x(1-x)[r_1(x, A(n)) - r_2(x, A(n))], \\ \dot{n} &= n(1-n)f(x),\end{aligned}$$



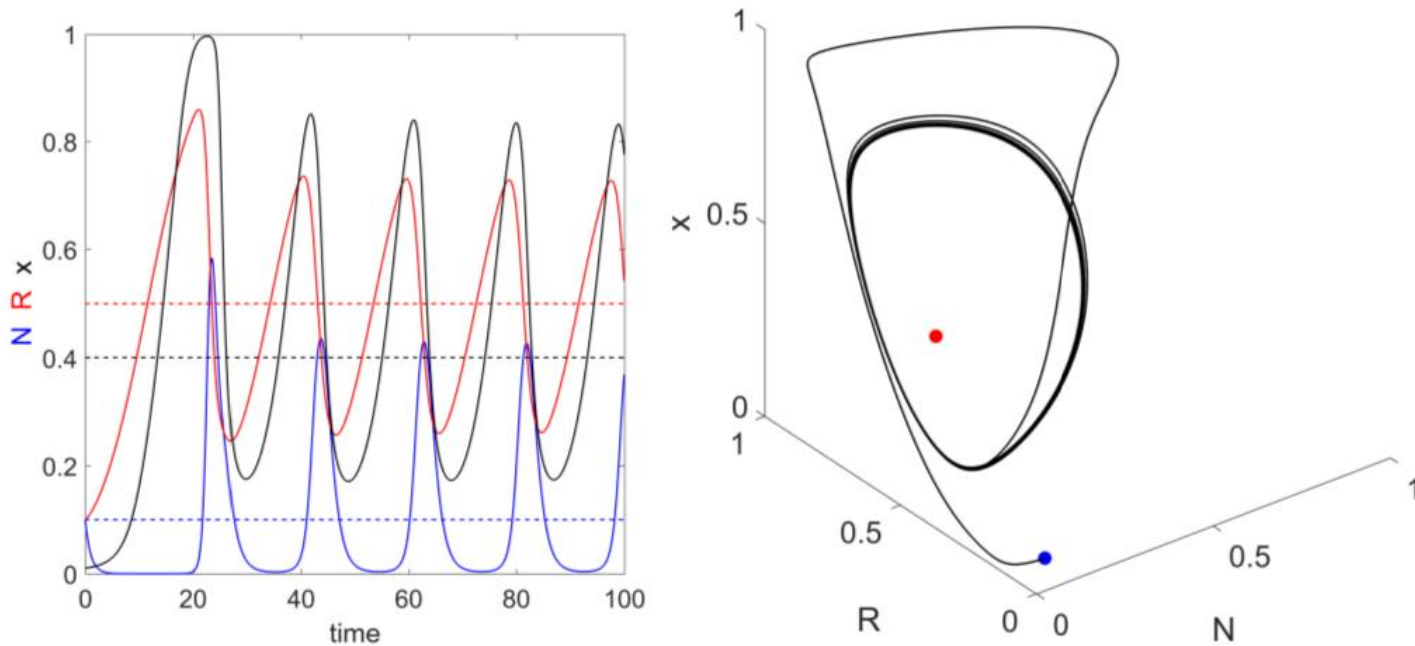
J.S. Weitz et al.

An oscillating tragedy of the commons in replicator dynamics with game-environment feedback. PNAS (2010)

Ongoing work

1. Eco-evolutionary role of solitary cell

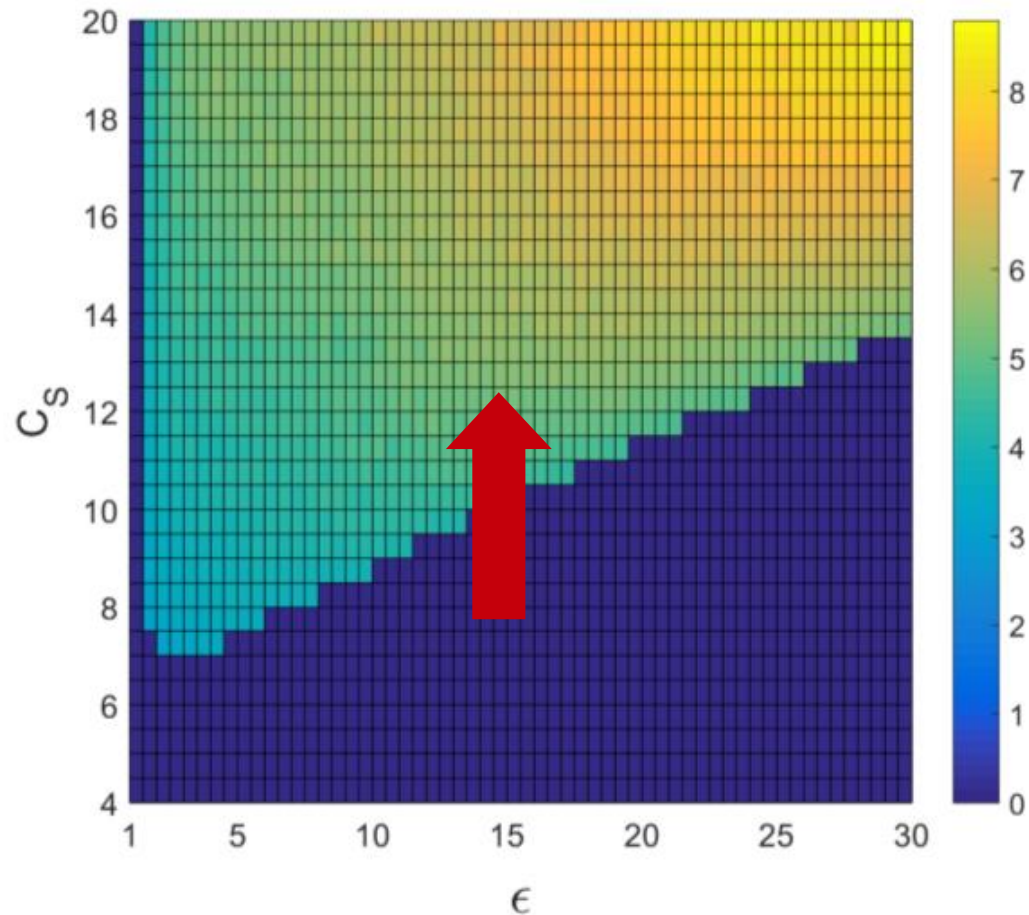
$$\begin{cases} \dot{R} = R[a(s - R) - N] \\ \dot{N} = N[\bar{p}(x)R - d] \\ \epsilon \dot{x} = x(1 - x)[p_F(x, R) - p_S(x, R)] \end{cases}$$



Leonardo Miele

Ongoing work

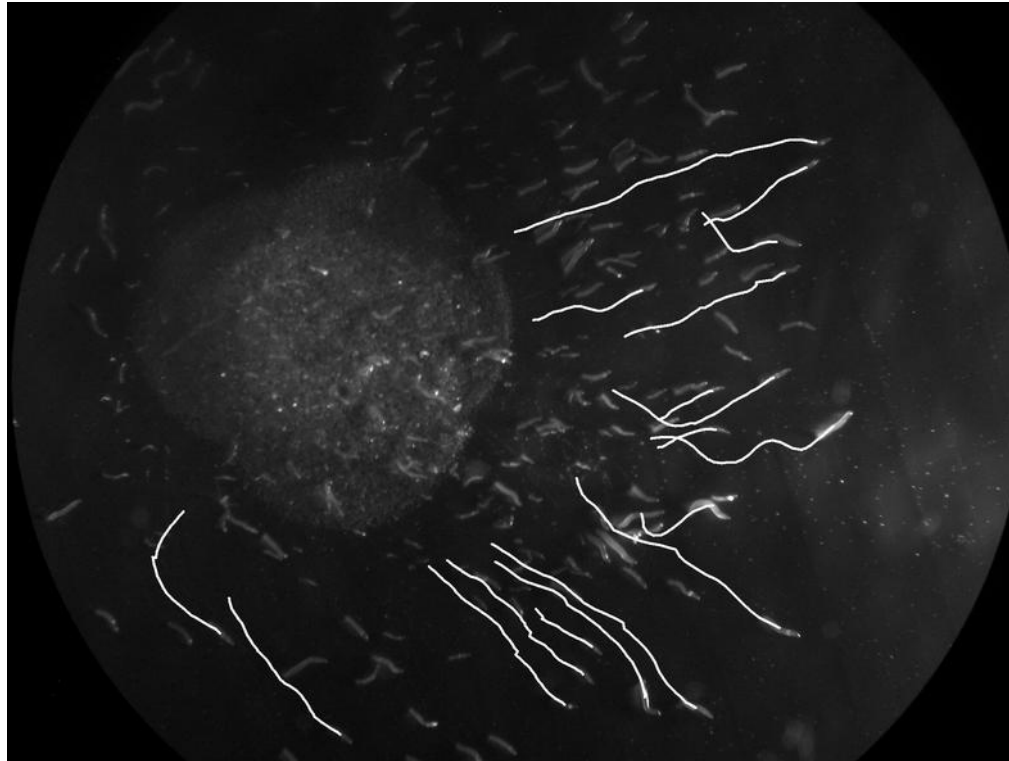
1. Eco-evolutionary role of solitary cell



Evolution drives the system towards a cyclic coexistence of types with different social strategy

Ongoing work

2. Phototactic behaviour in Dictyostelium



Clément Nizak (ESPCI), Felix
Geoffroy, Felix Foutel Roudier

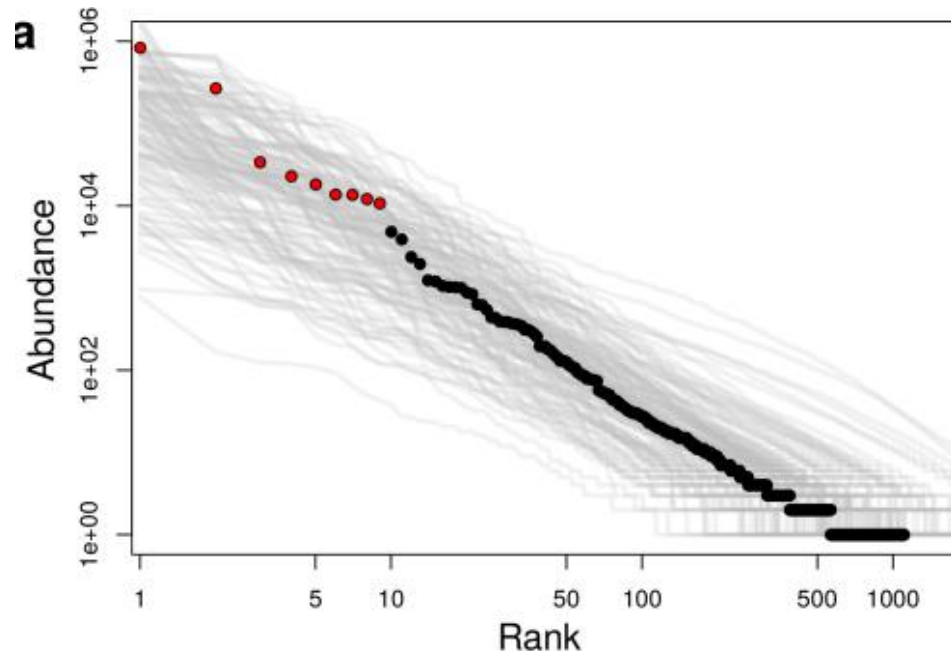
Ongoing work

3. Species Abundance Distributions in marine plankton protist communities



Global-scale sampling and sequencing with uniform protocol (121 stations, 388 samples).

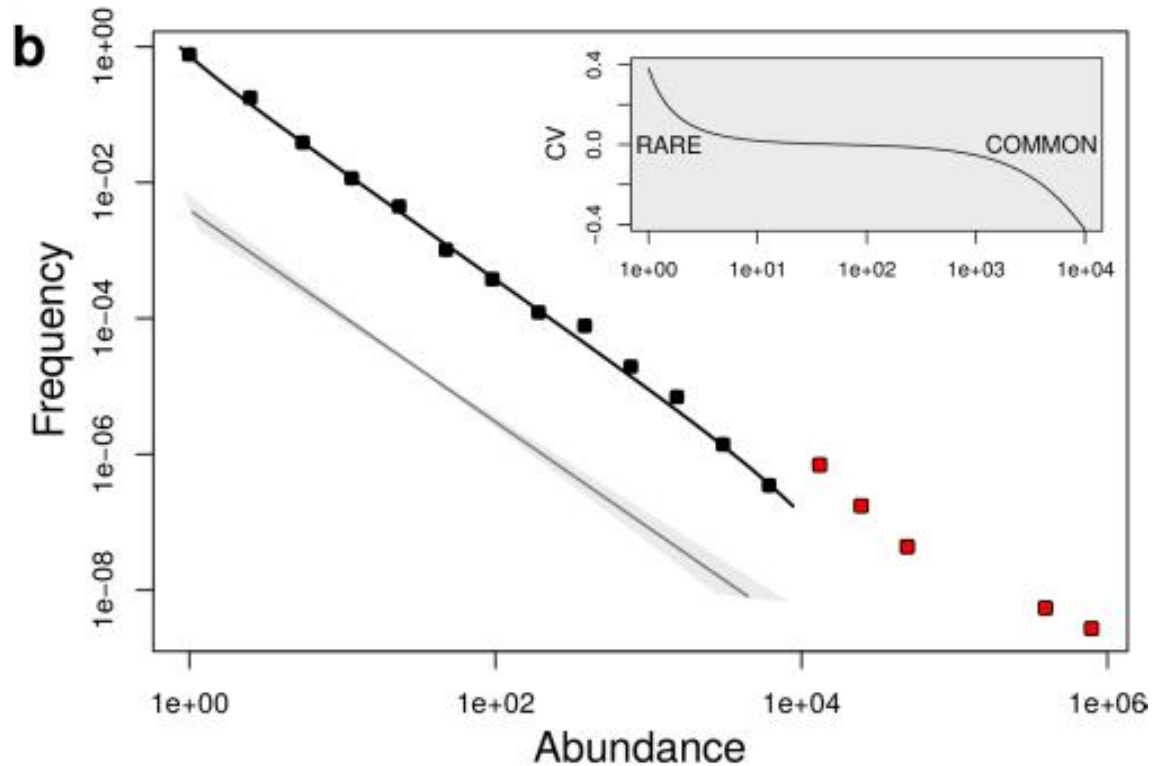
Meta-barcoding (V9) data for marine protists.



Enrico Ser-Giacomi, Lucie Zinger, Shruti Malviya, Colomaban de Vargas, Eric Karsenti, Chris Bowler

Ongoing work

3. Species Abundance Distributions in marine plankton protist communities

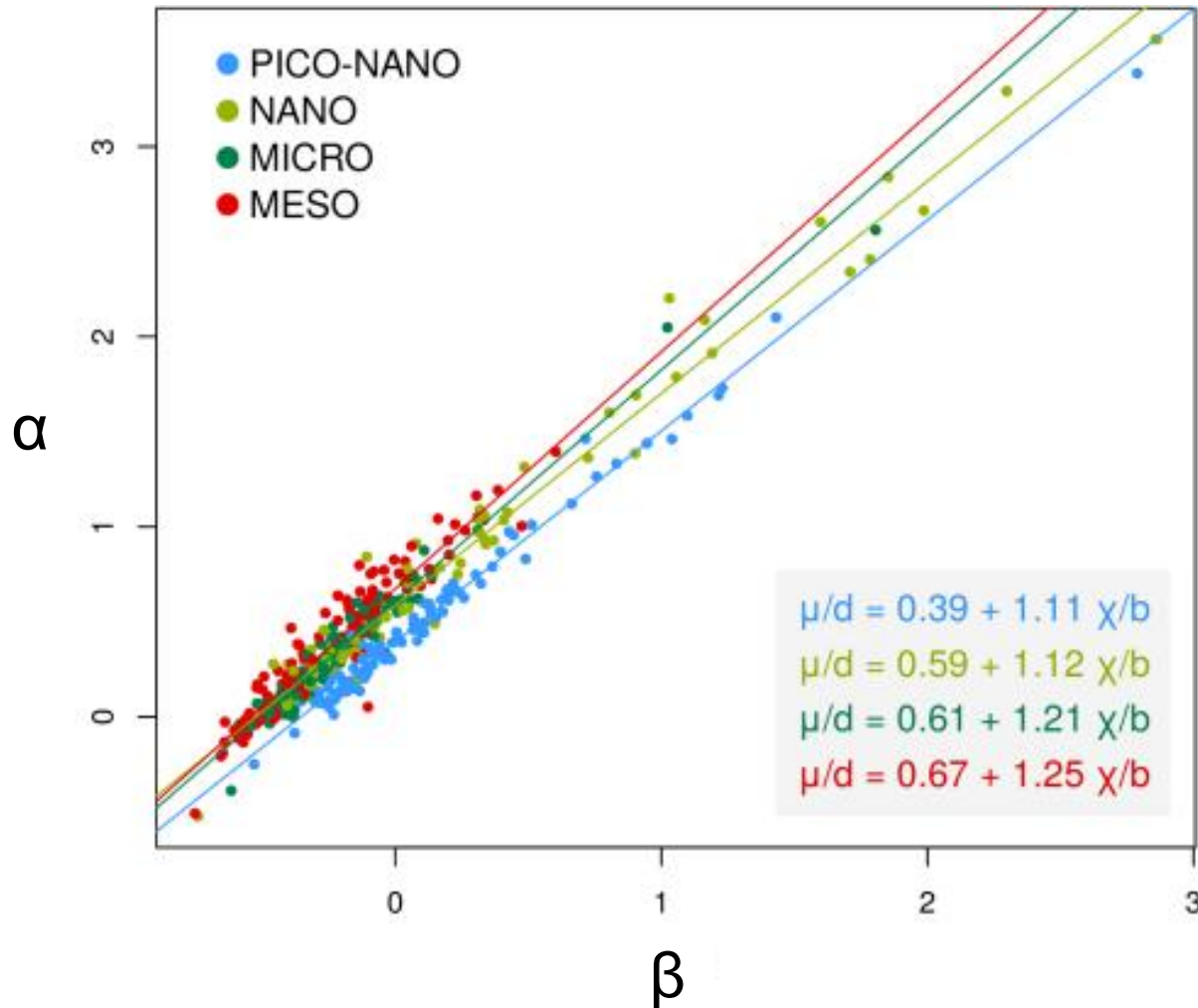


$$\langle \phi_n \rangle = \theta \frac{\Gamma(n+\alpha)\Gamma(1+\beta)}{\Gamma(\alpha)\Gamma(n+\beta+1)} e^{-rn} \sim H n^{-\lambda} e^{-rn}$$

$$\lambda = 1 - \alpha + \beta$$

Ongoing work

3. Species Abundance Distributions in marine plankton protist communities

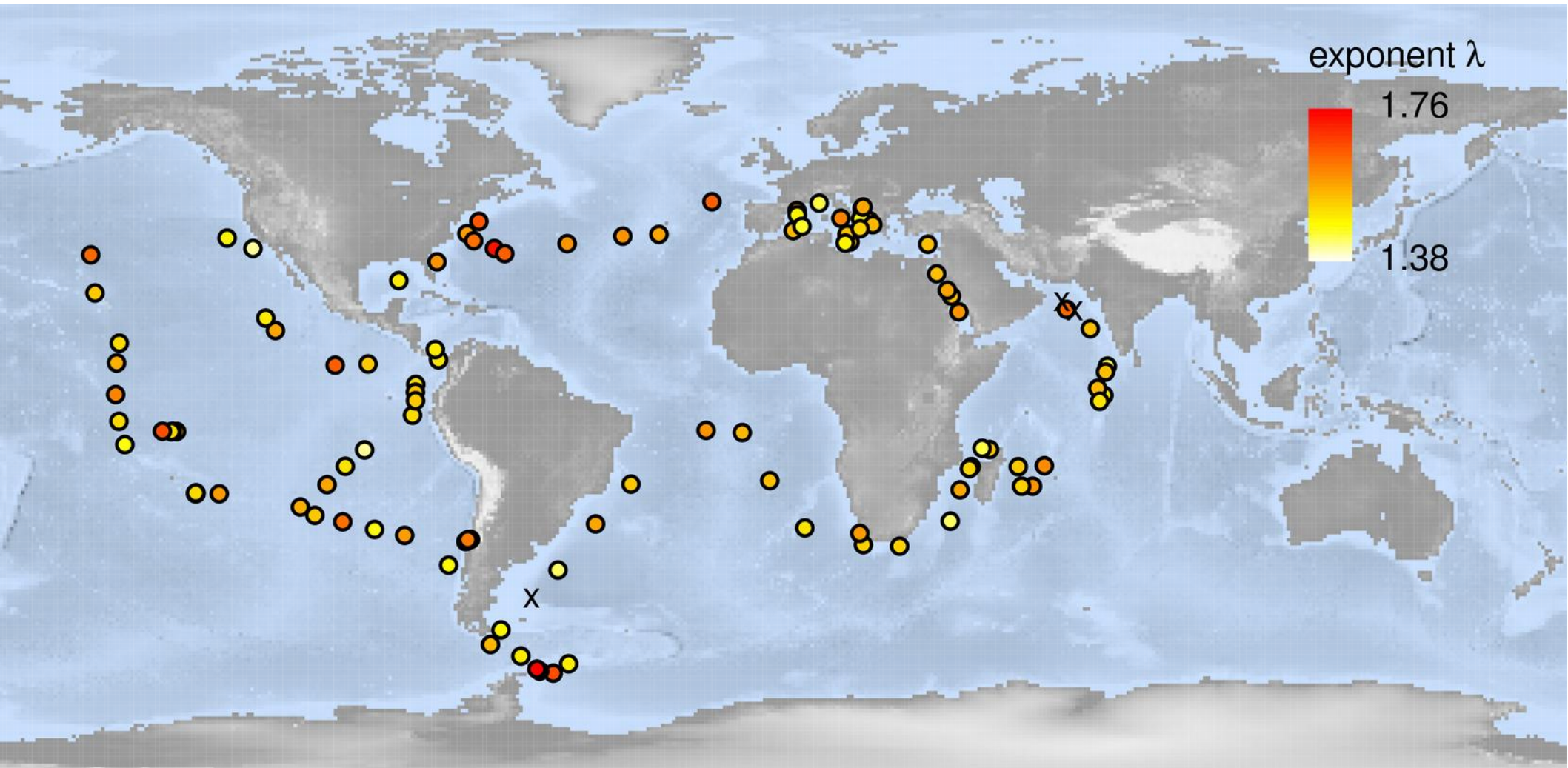


Small variation (<10%) of the exponent of the abundance decay for non-dominant OTUs

No biogeographical pattern detected

Ongoing work

3. Species Abundance Distributions in marine plankton protist communities



Microbes, evolution, multicellularity

Paul Rainey (ESPCI, NZIAS, MPI)

Modelling

Thomas Garcia (Collège de France)

Guilhem Doulcier (ESPCI)

Leonardo Miele (UPMC)

Felix Foutel Roudier (IBENS)

Thanks

Dicty experiments

Sandrine Adiba (IBENS)

Clément Nizak (ESPCI)

Felix Geoffroy (AgroParisTech)

Charles Bernard (AIV)

Plankton communities

Enrico Ser-Giacomi (IBENS)

Lucie Zinger (IBENS)

Shruti Malviya (NCBS, Bangalore)

Chris Bowler (IBENS)

Tara Oceans consortium