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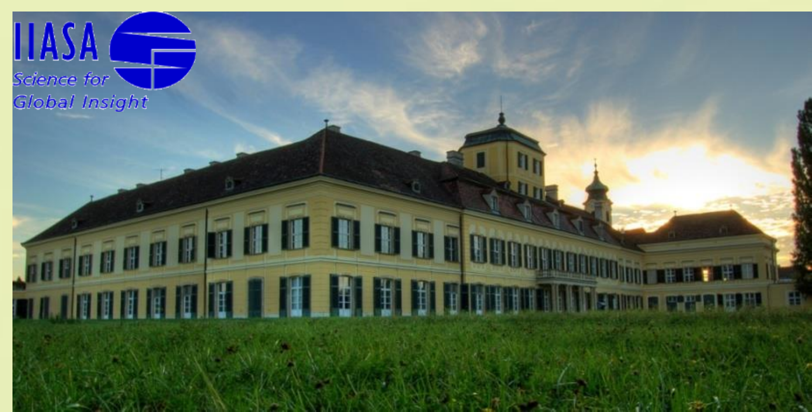
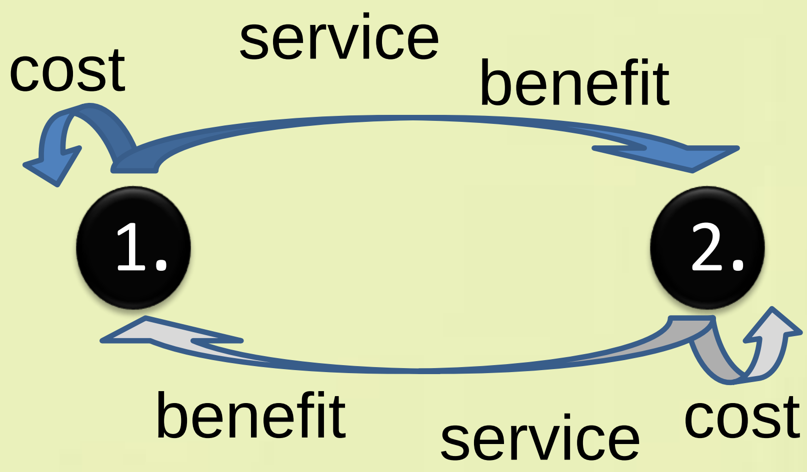


I am interested in...

- The evolution and stability of mutualism and cooperation
- Continuous reactive investment games
- Conditional, context-dependent cooperation
- Partner choice mechanisms
- Public Good Games with threshold effects
- Division of labor in collective actions
- Stability of microbiomes
- Quorum sensing
- Coexistence and cooperation in early replicator communities

Direct reciprocity

Interacting individuals



Reciprocity in humans: Economic exchanges

Reciprocity in humans:
food sharing among hunter-gatheres
(Aché in Paraguay)

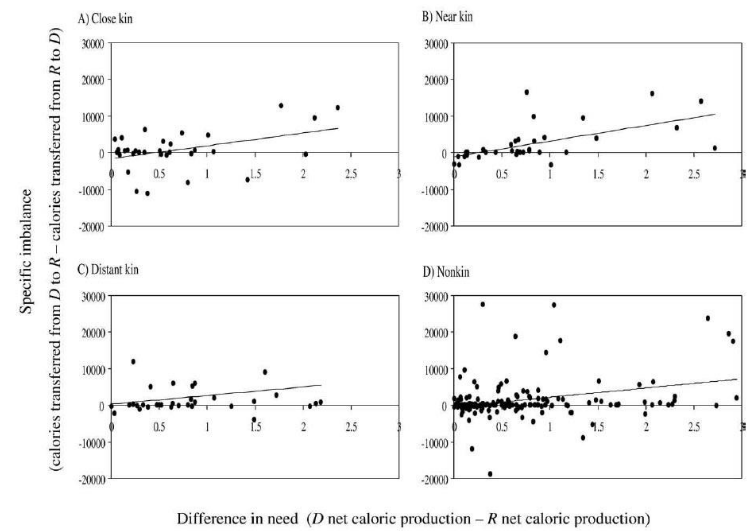


Fig. 1. Linear regression of the relationship between the difference in net caloric production between dyads of households and specific imbalance in their food transfers (arrayed so that positive specific imbalance values are attained when an imbalance favors the household with the lower net caloric value). Plots for (a) close kin (r>.05), (b) near kin (.018<r<.047), (c) distant kin (0<r<.018), and (d) unrelated dyads (r=0).

Evolution and Human Behavior 29 (2008) 305–318

Reciprocal altruism, rather than kin selection, maintains nepotistic food transfers on an Ache reservation☆

Wesley Allen-Arave[a,*], Michael Gurven[b], Kim Hill[c]

[a]Department of Anthropology, University of New Mexico, Albuquerque, NM 87131, USA
[b]Department of Anthropology, University of California Santa Barbara, Santa Barbara, CA 93106, USA
[c]School of Human Evolution and Social Change, Arizona State University, Tempe, AZ 85287, USA

Initial receipt 9 December 2006; final revision received 24 March 2008

Reciprocity in animals: food sharing in vampire bats (*Desmodus rotundus*)

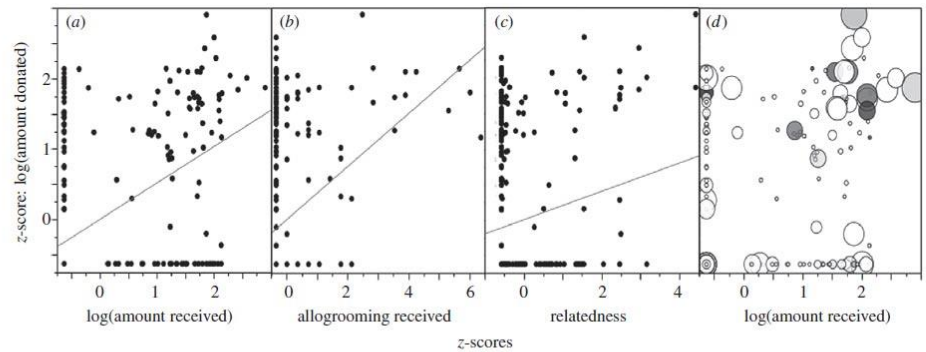


Figure 1. Relationships between food donated and predictor variables. *z*-score for log food donated was predicted by *z*-scores of (*a*) log food received ($R^2 = 0.27$, $p < 0.0002$), (*b*) allogrooming received ($R^2 = 0.14$, $p < 0.0002$) and (*c*) relatedness ($R^2 = 0.04$, $p < 0.0012$). A bubble plot (*d*) shows multivariate relationships by scaling bubble size to relatedness and bubble darkness to allogrooming received.

Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment

Gerald G. Carter and Gerald S. Wilkinson

Proc. R. Soc. B 2013 **280**, 20122573, published online 2 January 2013

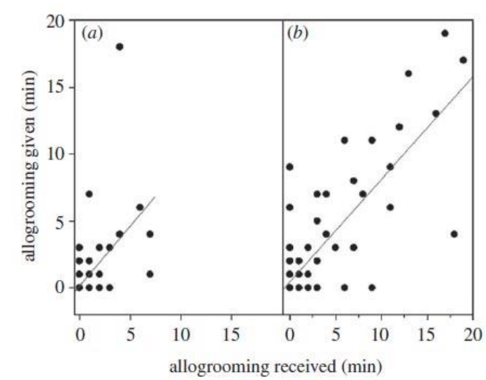
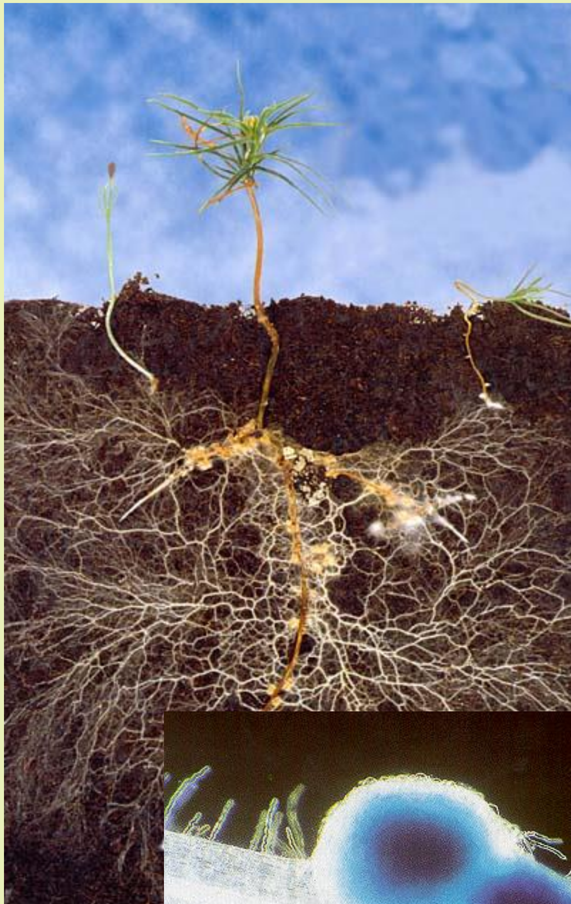
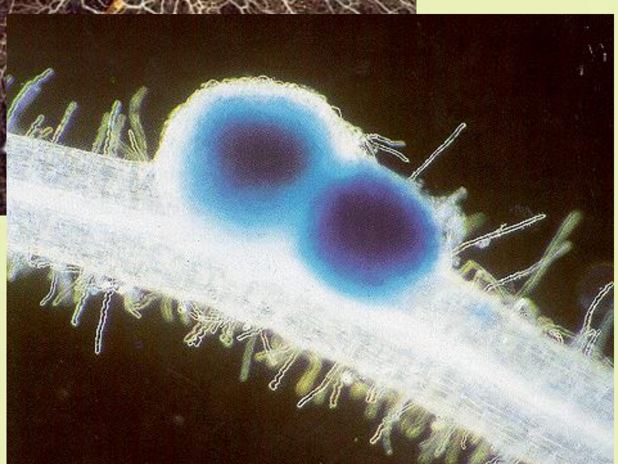
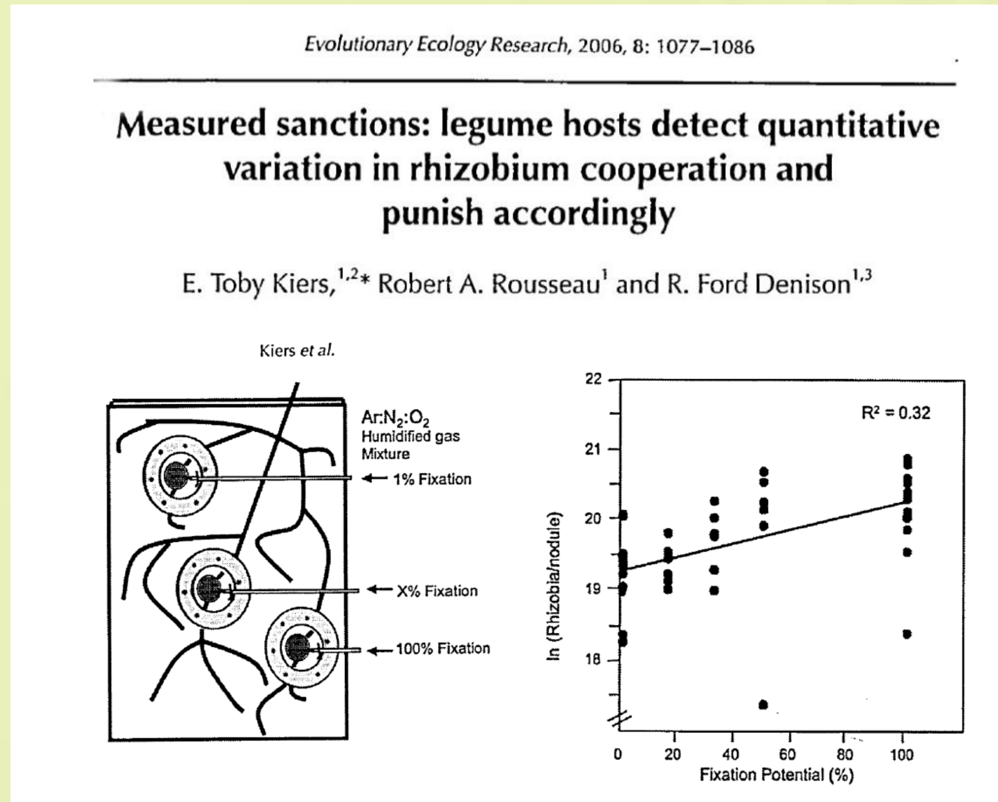


Figure 3. Allogrooming given correlates with allogrooming received. Allogrooming giving is plotted against allogrooming received for dyads that did not share food ((*a*) $n = 214$, $r = 0.62$, $p < 0.0002$) and dyads that did share food ((*b*) $n = 98$, $r = 0.81$, $p < 0.0002$). On non-trial days, dyads that shared food both gave and received more allogrooming than non-sharing dyads ($F_{1,310} = 32.9$ and 41.0, $p < 0.0002$ for both).

Reciprocity in plants, fungi, bacteria: nutritional mutualisms





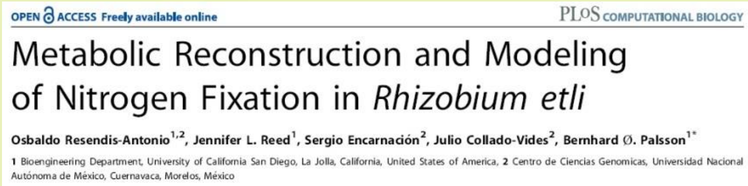


Evolutionary Ecology Research, 2006, 8: 1077–1086

Measured sanctions: legume hosts detect quantitative variation in rhizobium cooperation and punish accordingly

E. Toby Kiers,[1,2]* Robert A. Rousseau[1] and R. Ford Denison[1,3]

Conditional mutualistic investments



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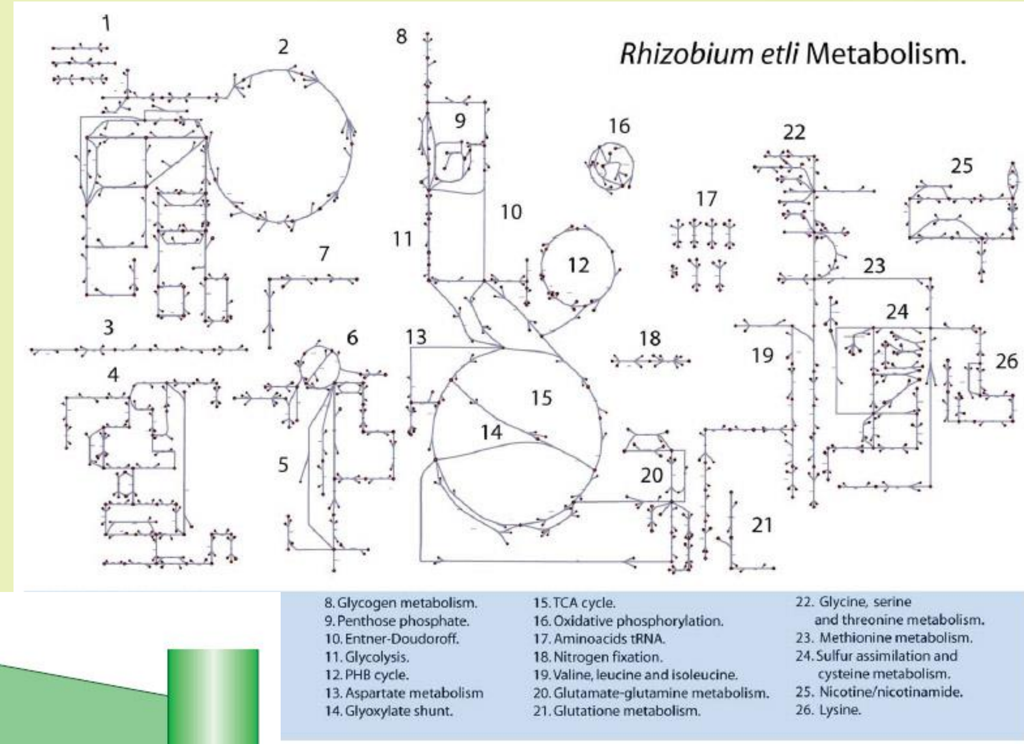
Metabolic Reconstruction and Modeling of Nitrogen Fixation in *Rhizobium etli*

Osbaldo Resendis-Antonio[1,2], Jennifer L. Reed[1], Sergio Encarnación[2], Julio Collado-Vides[2], Bernhard Ø. Palsson[1*]

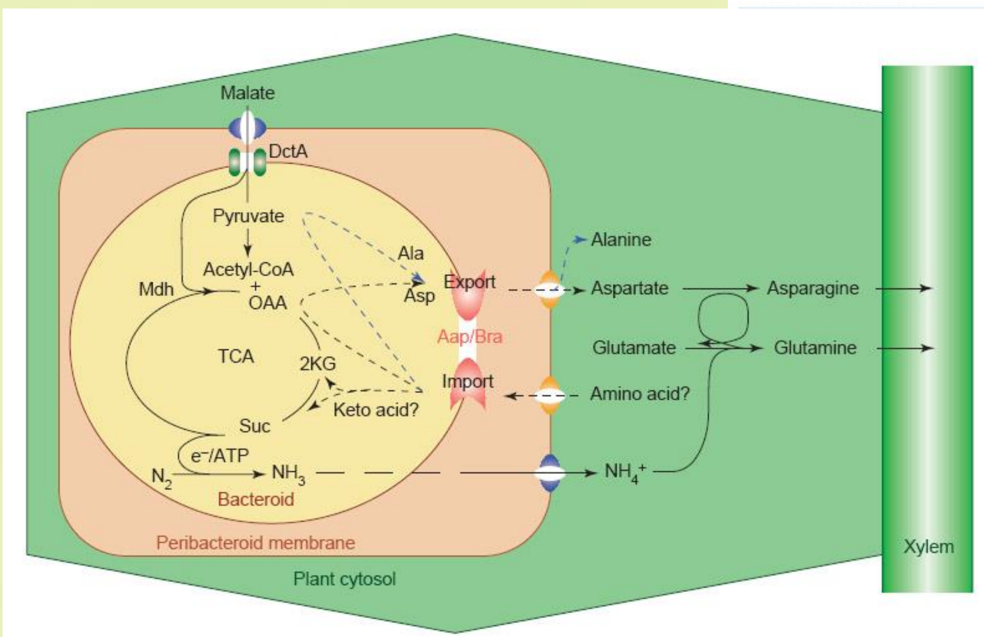
1 Bioengineering Department, University of California San Diego, La Jolla, California, United States of America, 2 Centro de Ciencias Genomicas, Universidad Nacional Autónoma de México, Cuernavaca, Morelos, México



Rhizobium etli

Analysis of the metabolic network

- 387 reactions
- 371 metabolites
- 363 genes



Conditional mutualistic investments

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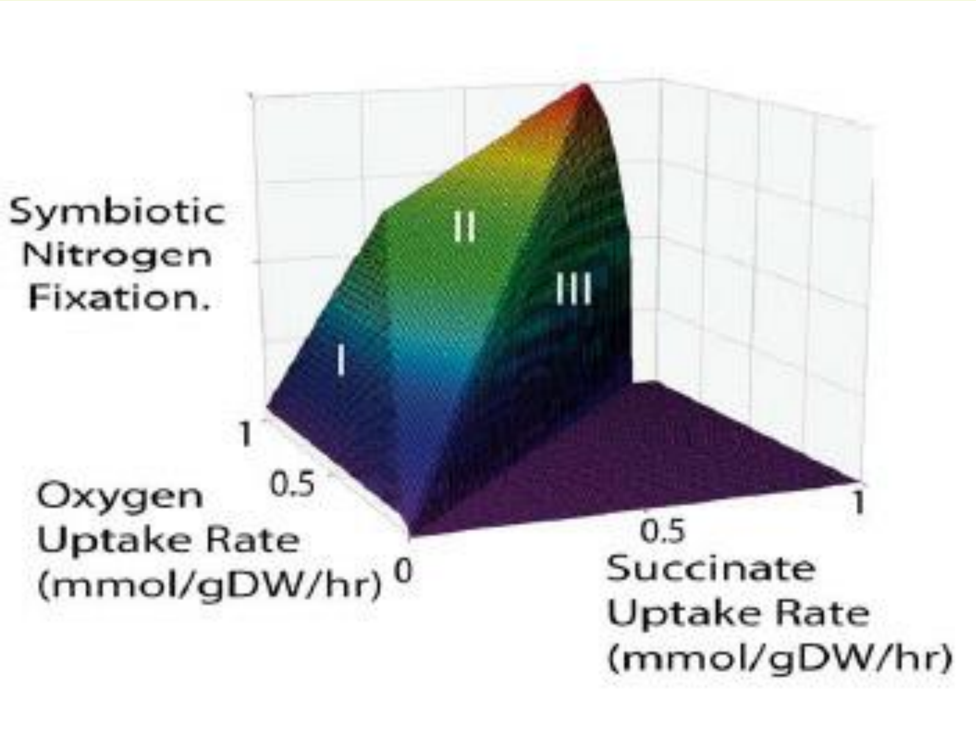
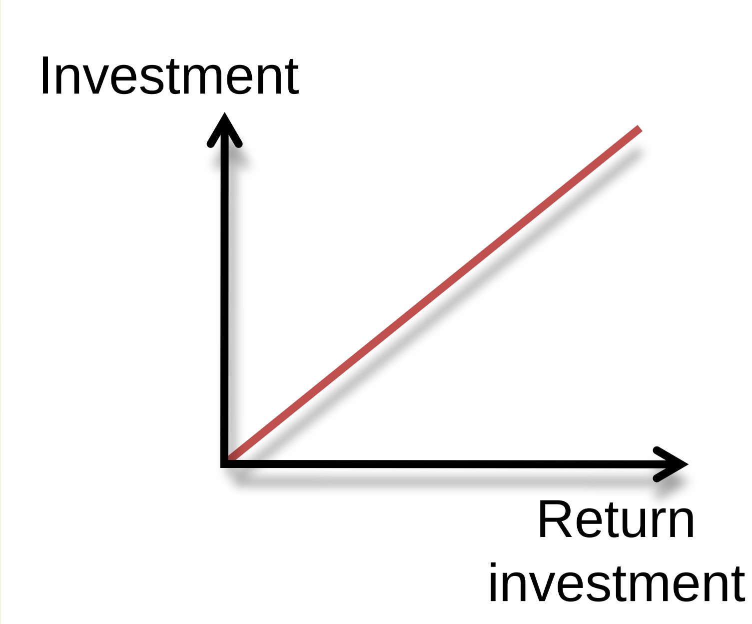




The model

$$I_{1,i,j} = u_i$$ Investment in the 1st round

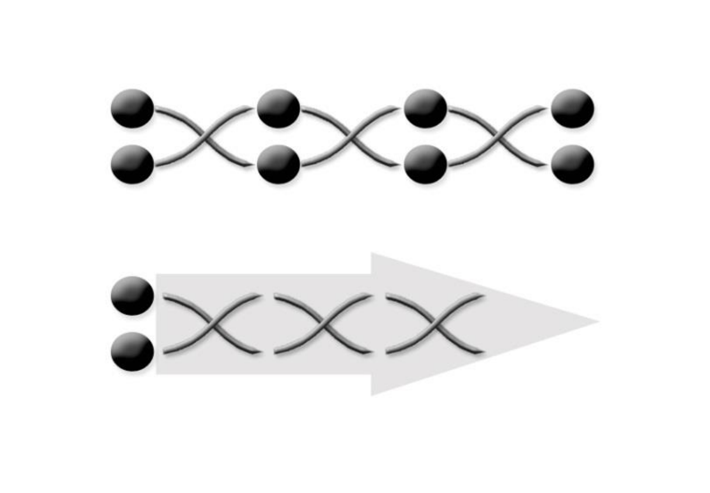
$$I_{t,i,j} = u_i + c_i p_{t-1,i,j}$$ Investment in the 1< rounds

$$C(I_{t,i,j}) = C_0 I_{t,i,j}$$

$$B(I_{t,j,i}) = B_0[1 - \exp(-B_1 I_{t,j,i})]$$

$$p_{t,i,j} = B(I_{t,j,i}) - C(I_{t,i,j})$$

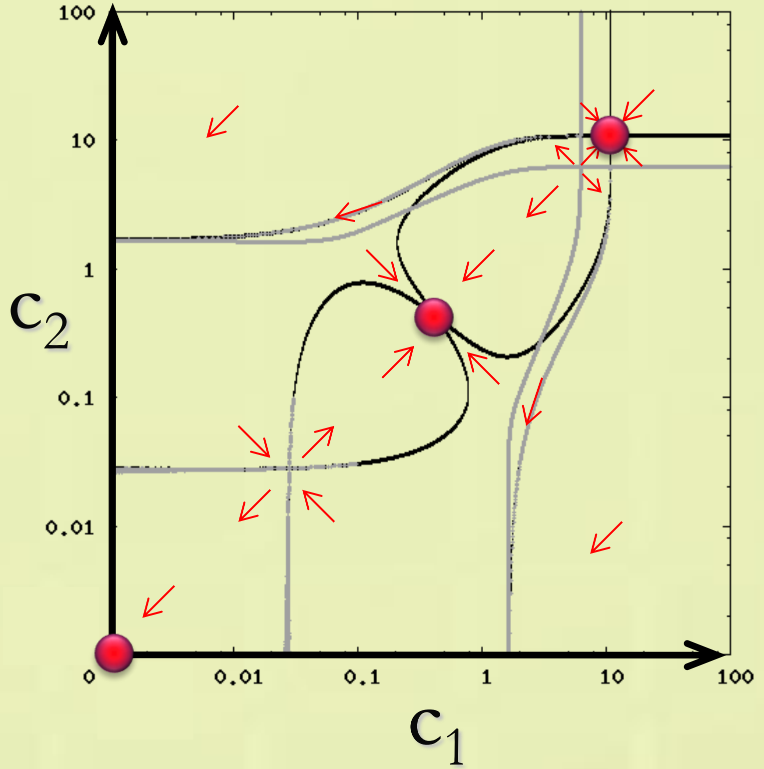
t >1, iterative game



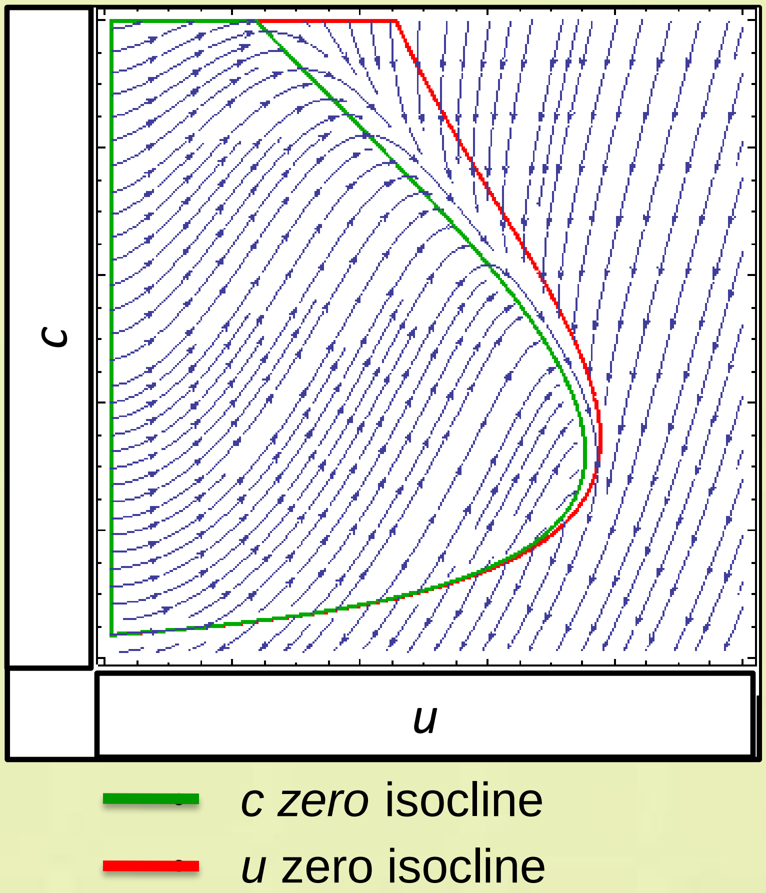
The evolution and stability of conditional investments

$$I_t = \alpha + c \bullet payoff_{t-1}$$

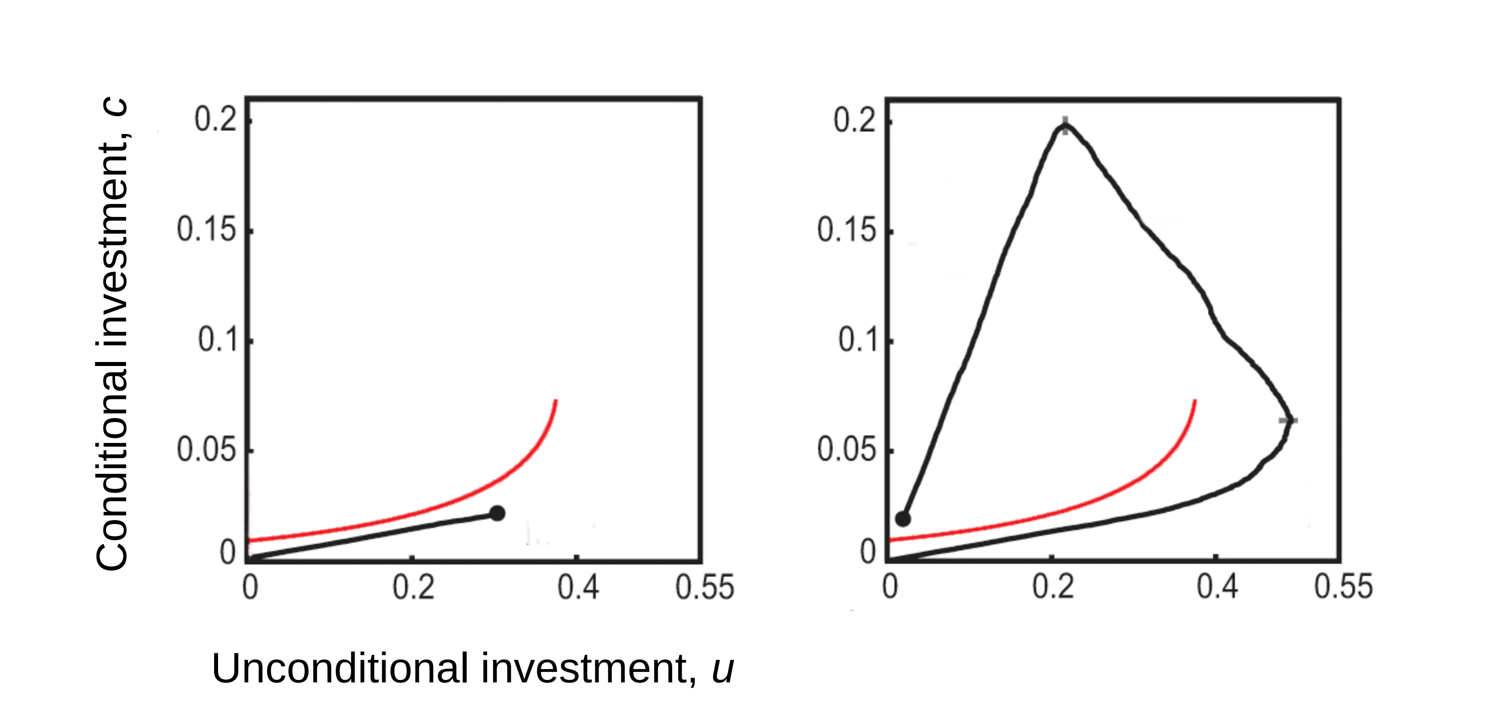
$\alpha_1 = \alpha_2 = \text{const.} > 0$



The evolution and stability of conditional and unconditional investments

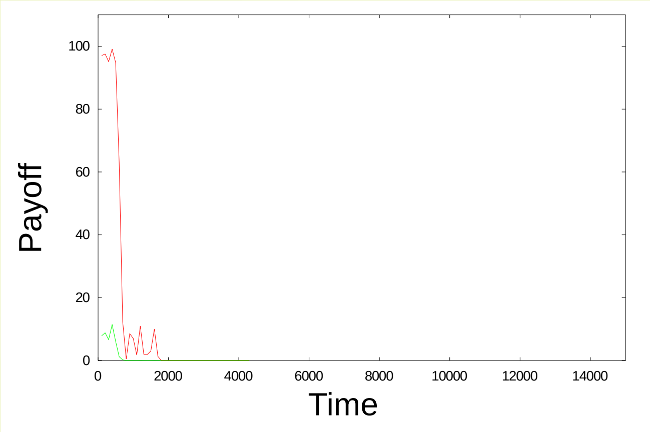


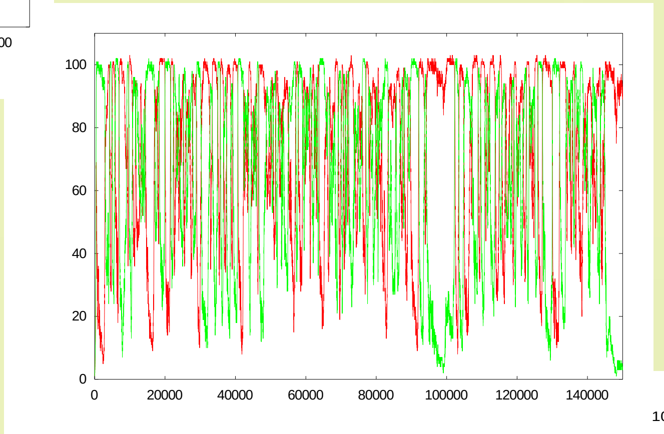
The investment cycle

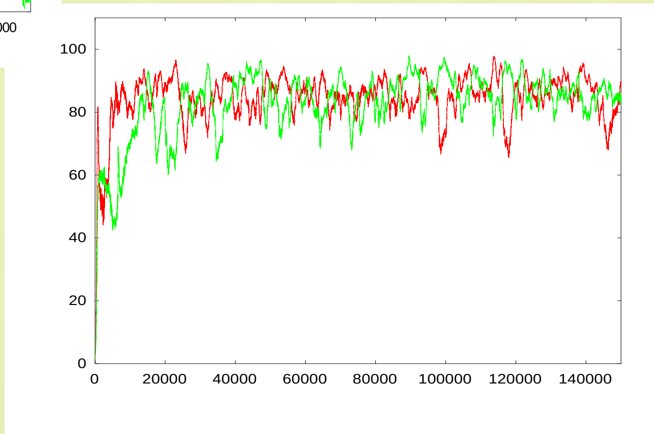


(closely) monomorphic population

IBM simulation results

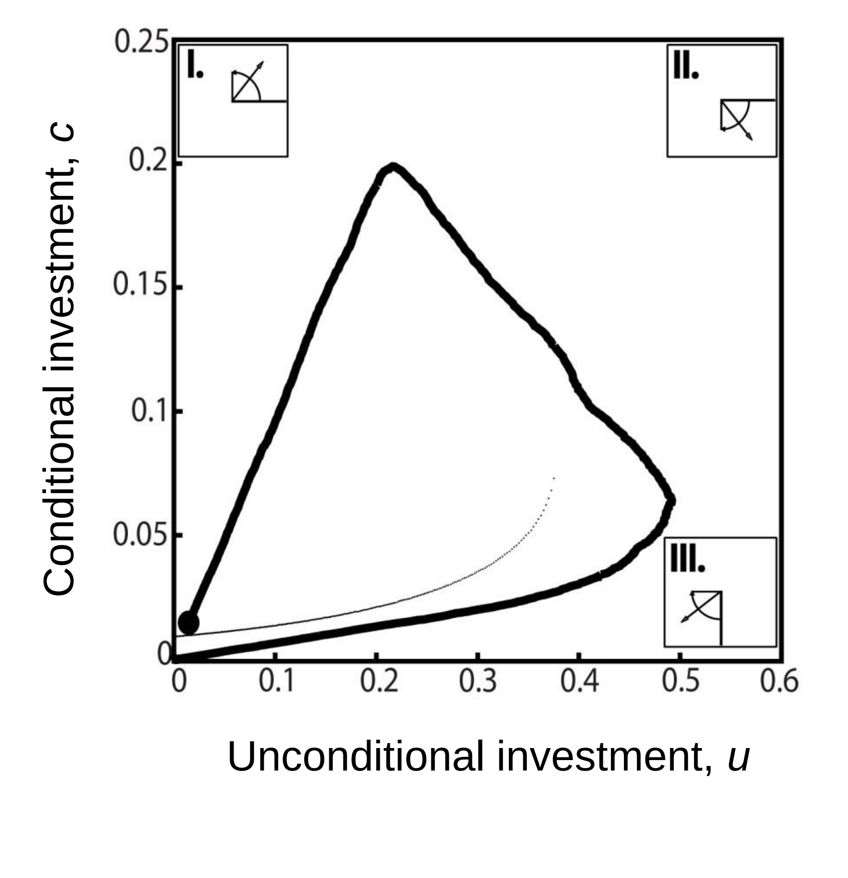






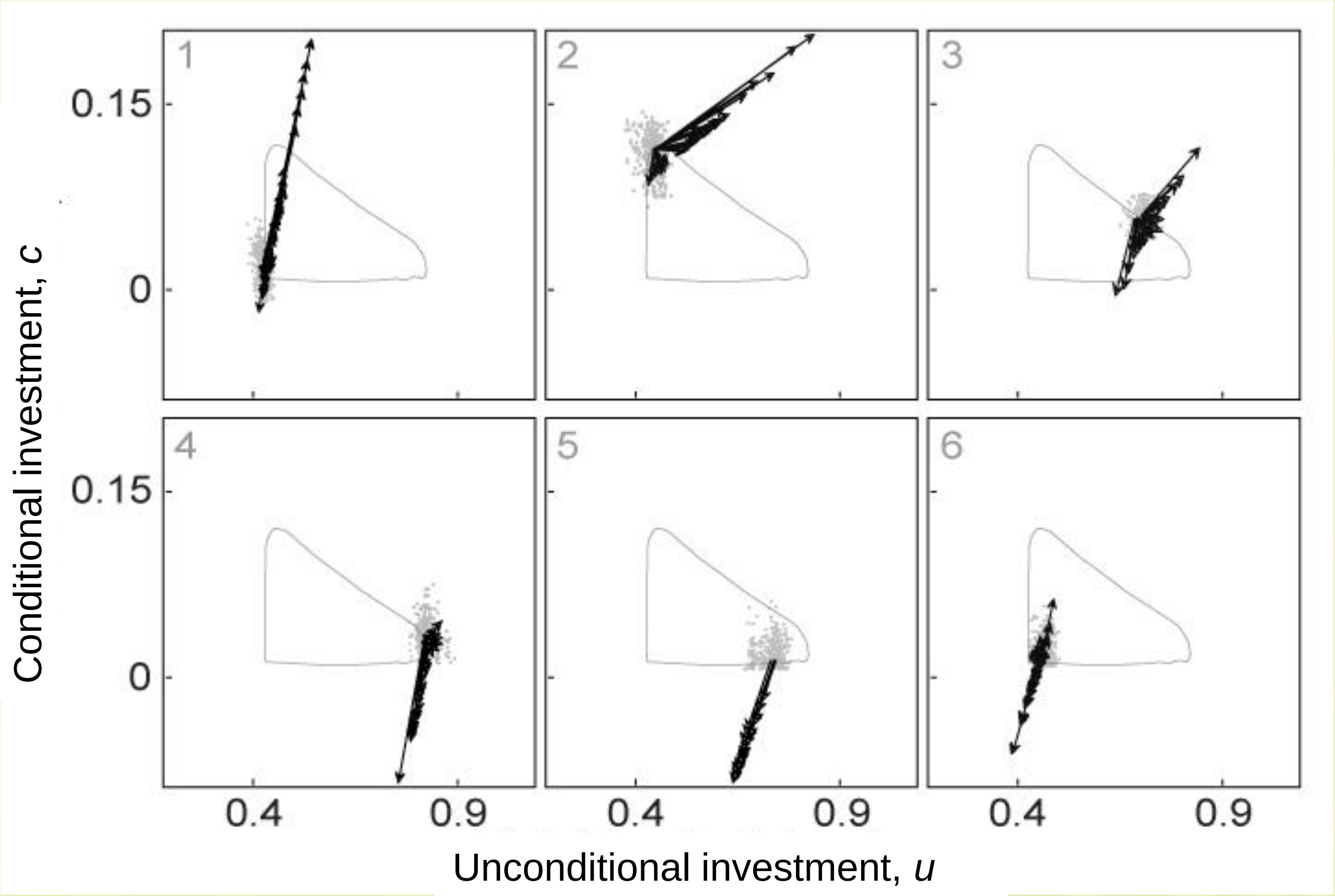
Investment cycle phases

$$g_{i,x}(x_i) = \partial \left(\frac{1}{J} \sum_{j=1}^{J} P_{i,j} \right) \Big/ \partial x_i' \Big|_{x_i' = x_i}$$

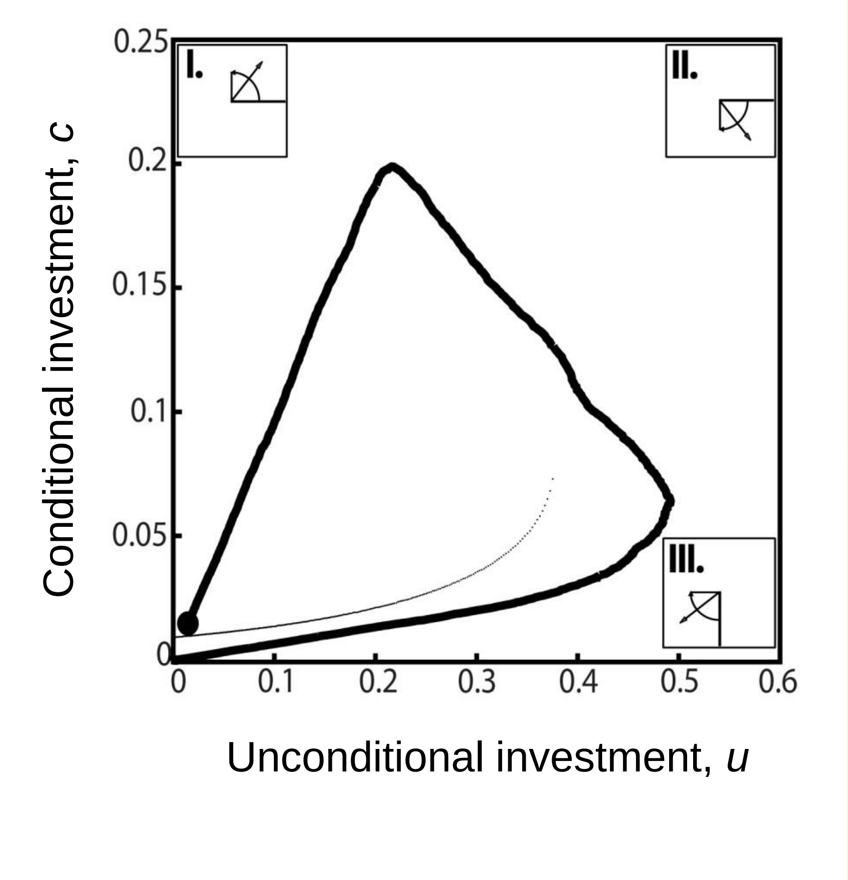


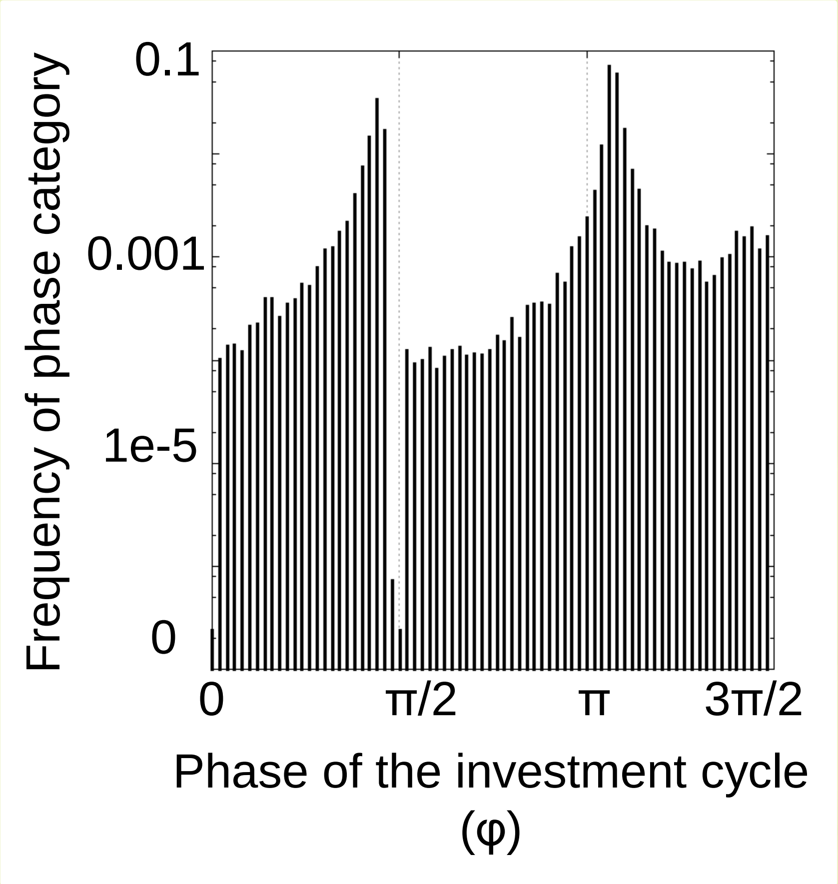
Investment cycle and phase polymorphism

$$g_{i,x}(x_i) = \partial\left(\frac{1}{J}\sum_{j=1}^{J} P_{i,j}\right) \Big/ \partial x_i' \Big|_{x_i'=x_i}$$

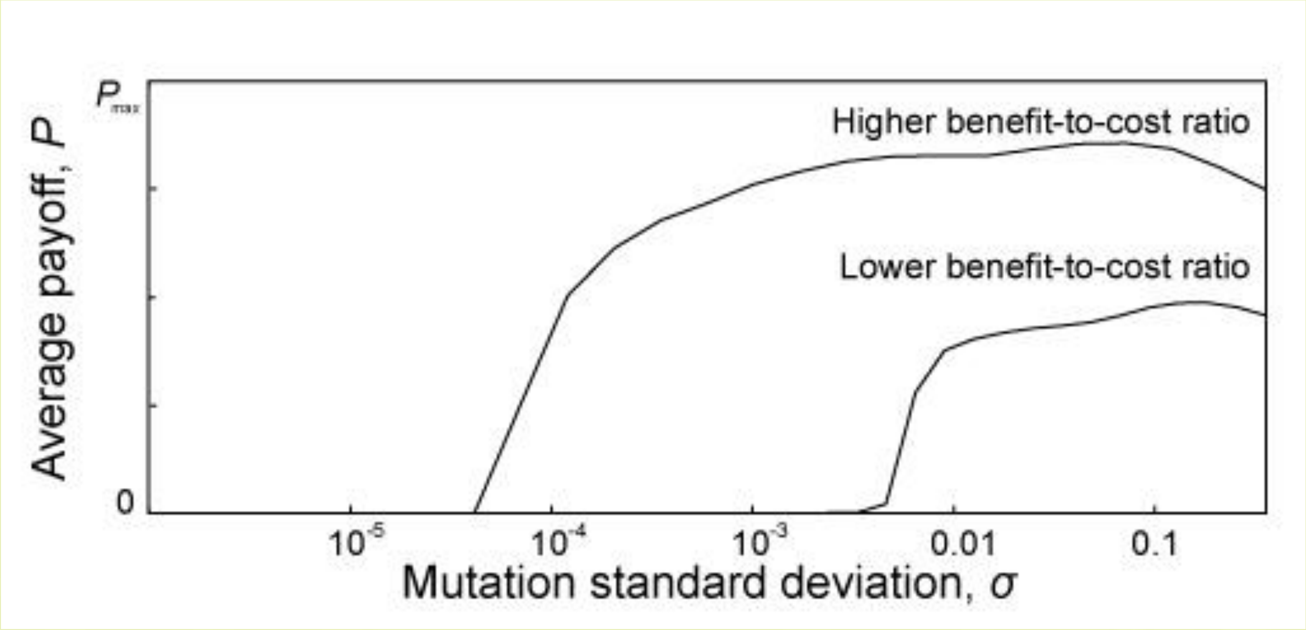


Investment cycle and phase polymorphism

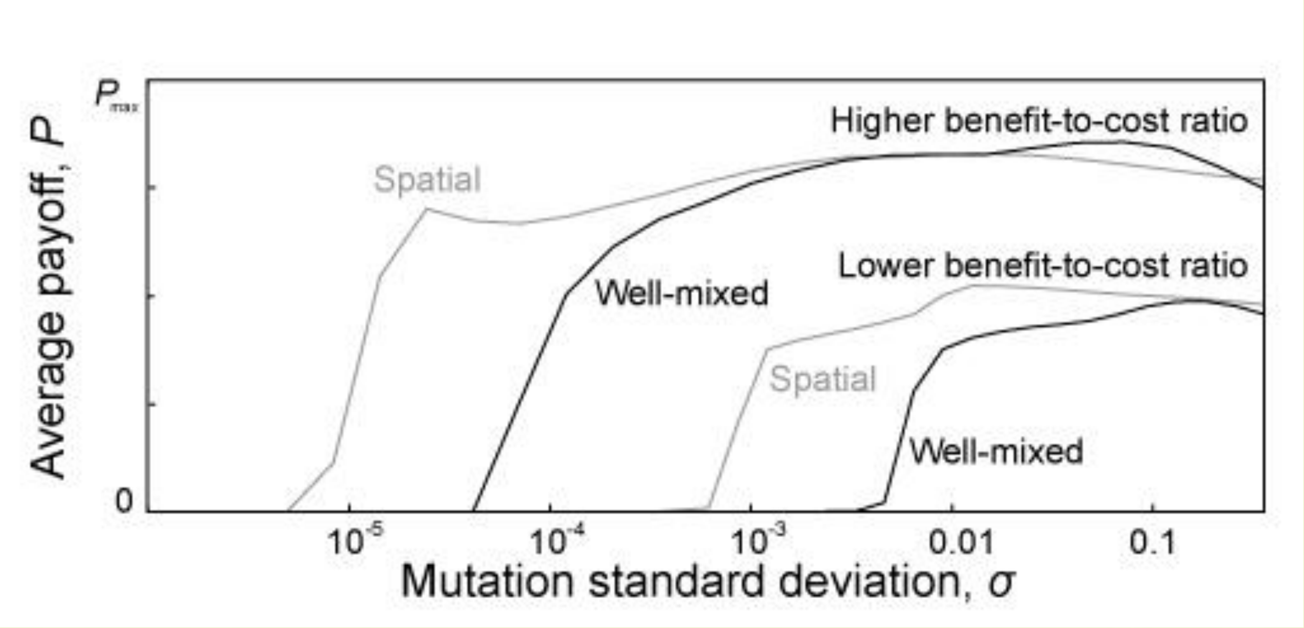




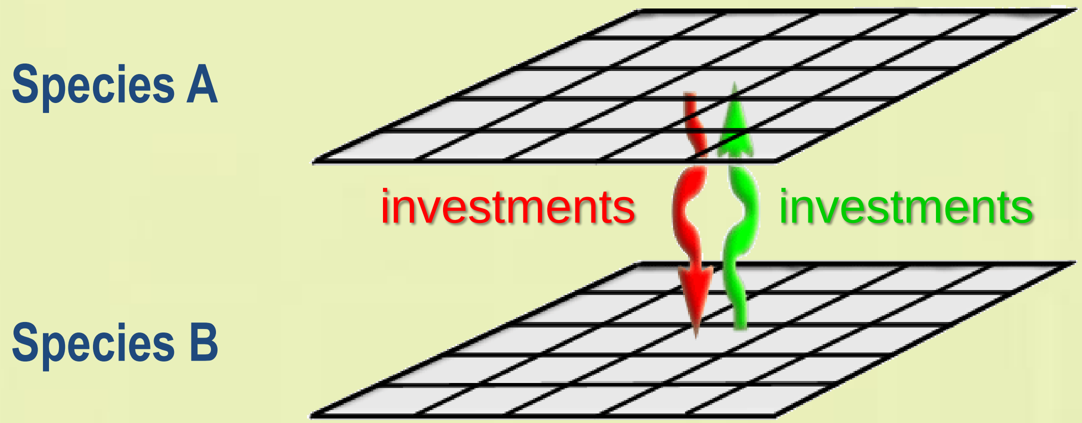
Strategy diversity and phase polymorphism stabilizes cooperative investments



Strategy diversity and phase polymorphism stabilizes cooperative investments

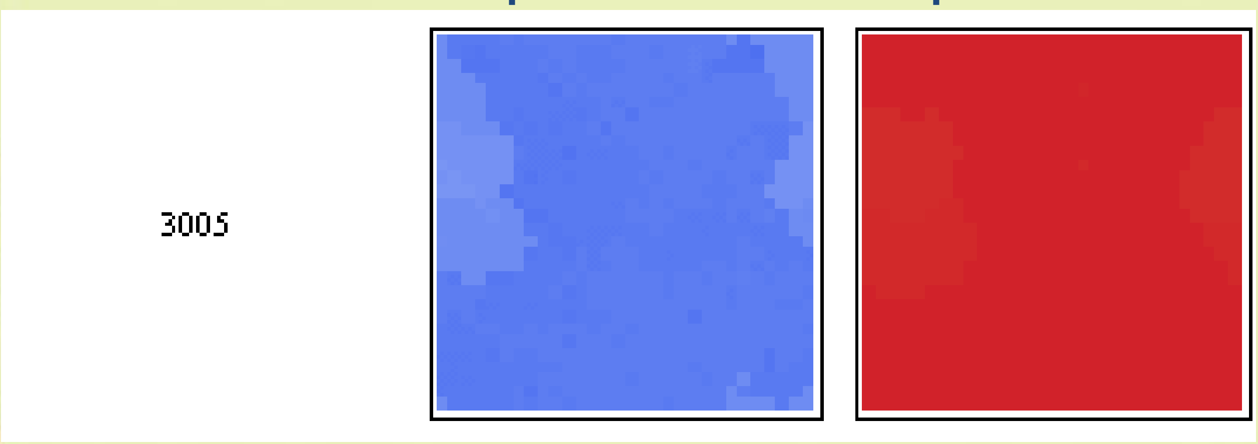


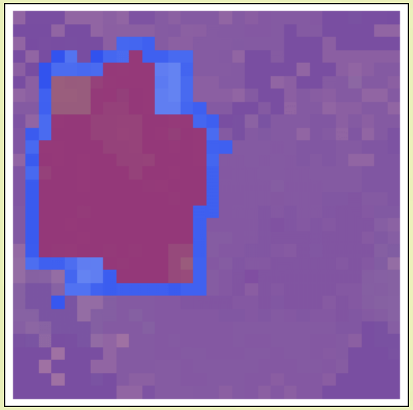
Introducing spatial population structure in interspecific reciprocal investment game



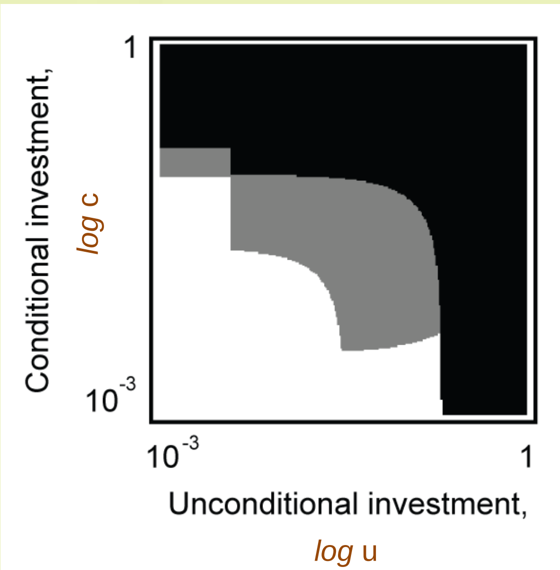
Spatial bubbles and the dynamic spatial mosaic structure

Species A Species B





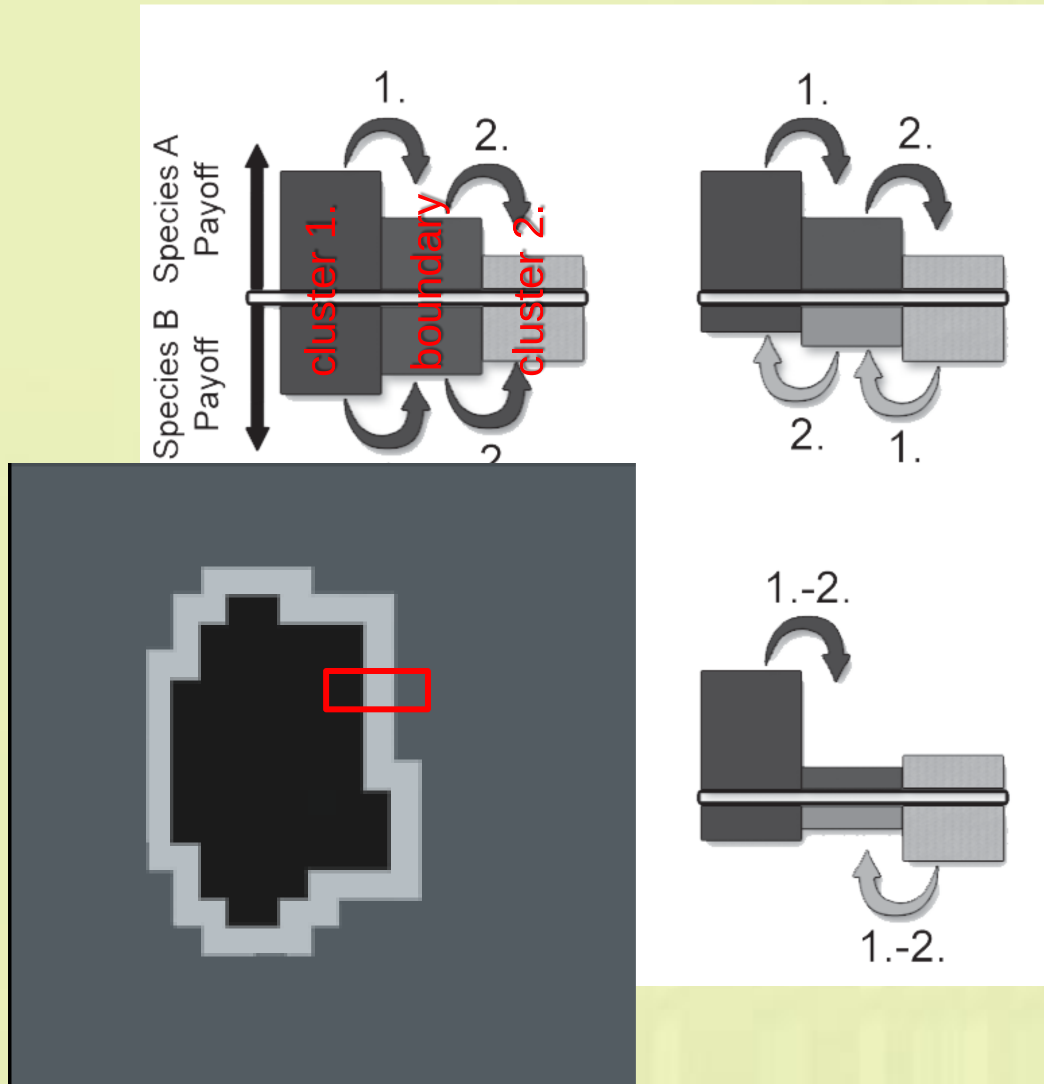
Spatial bubbles and invasion dynamics



m → R

coexistence

R → m



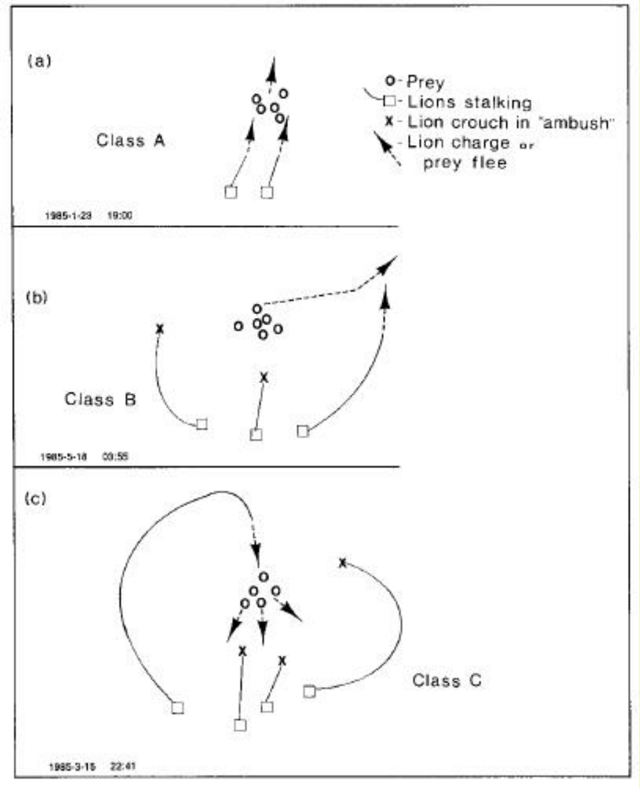
Summary

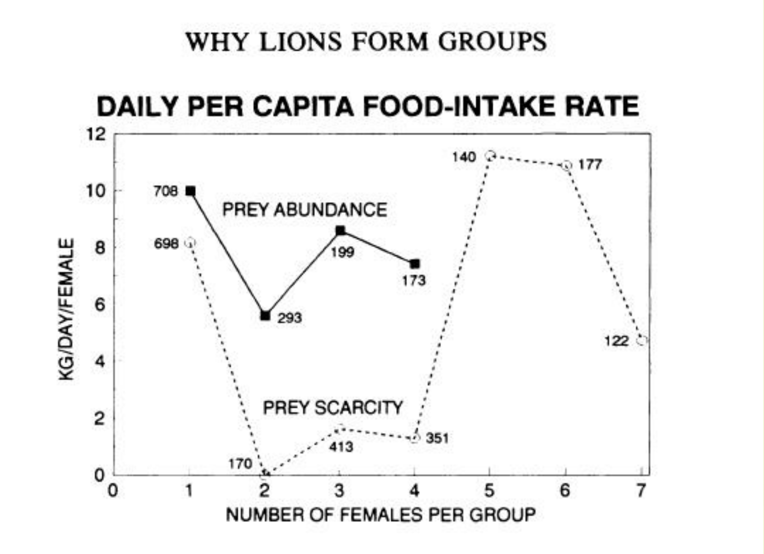
- Cooperative investments are unstable for medium levels of reciprocity
- Above a threshold, evolution drives strategy pairs through investment cycles temporarily
- Mutation-generated polymorphism of strategies leads to phase diffusion along the investment cycle
- Strategy diversity (polymorphism) stabilizes investment levels at the population level
- Spatial mosaic structure further promotes mutualism stability, through a mechanism that is fundamentally different from the role of space in intraspecies cooperation

Non-linear benefit functions

and threshold effects in nature

lions (*Panthera leo*)





from Packer *et al.* (1990)
and Stander (1992)

Non-linear benefit functions

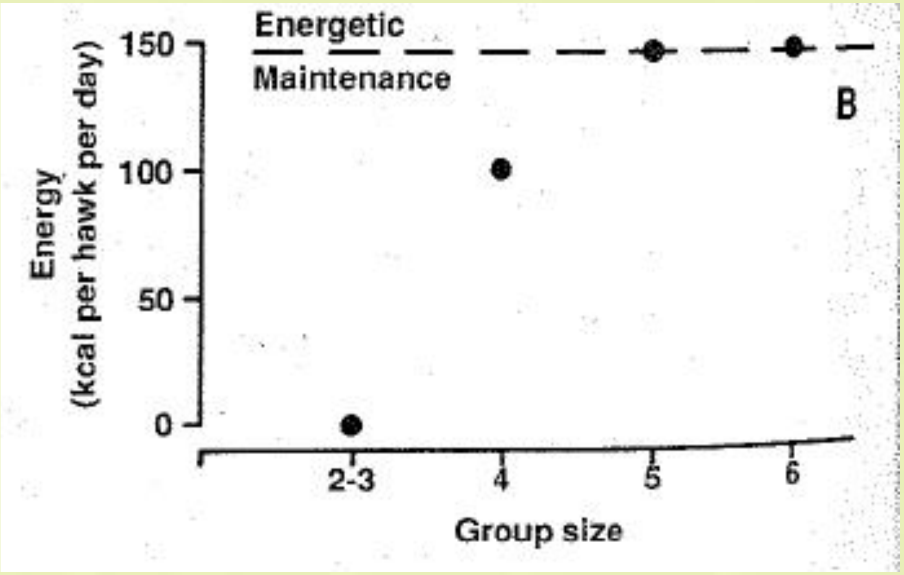
and threshold effects in nature

Harris' Hawk (*Parabuteo unicinctus*)

from Bednarz (1988)

Brown-Necked Raven (*Corvus ruficollis*)

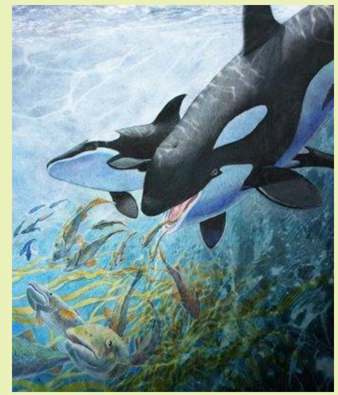
Yosef & Yosef (2009)

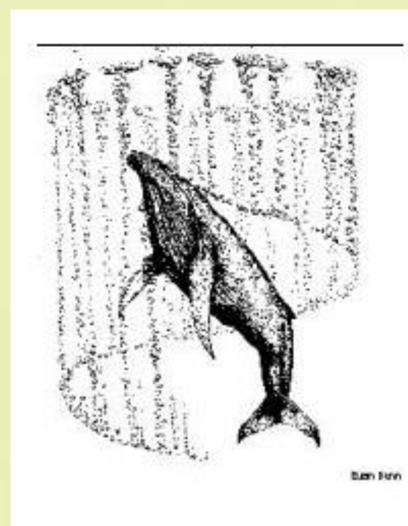


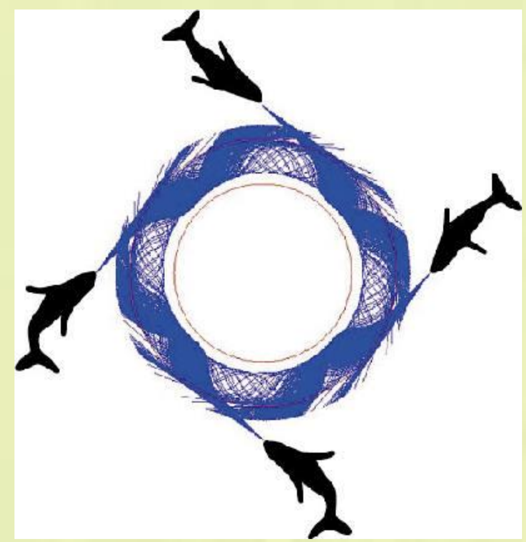
Non-linear benefit functions

and threshold effects in nature

killer whales (*Orcinus orca*)
humpback whales (*Megaptera novaengliae*)



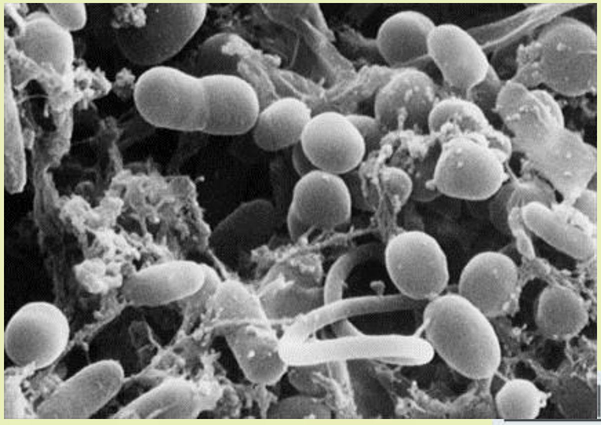


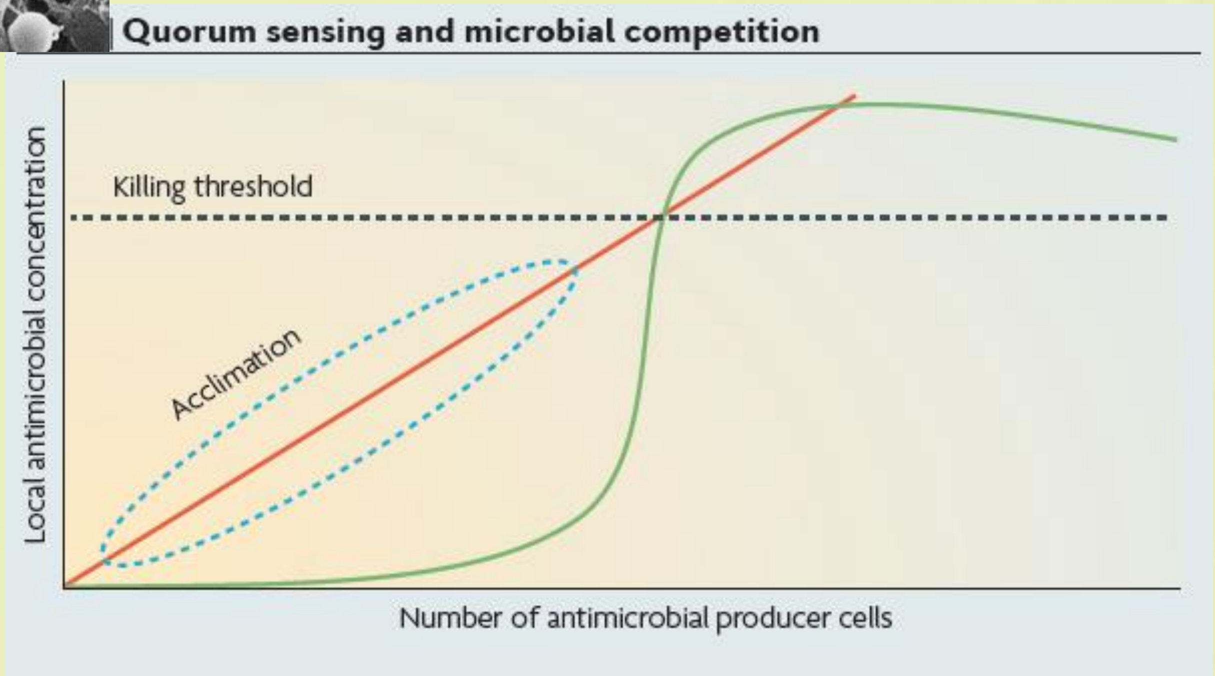


from Leighton *et al.* (2004)

Non-linear benefit functions

and threshold effects in nature

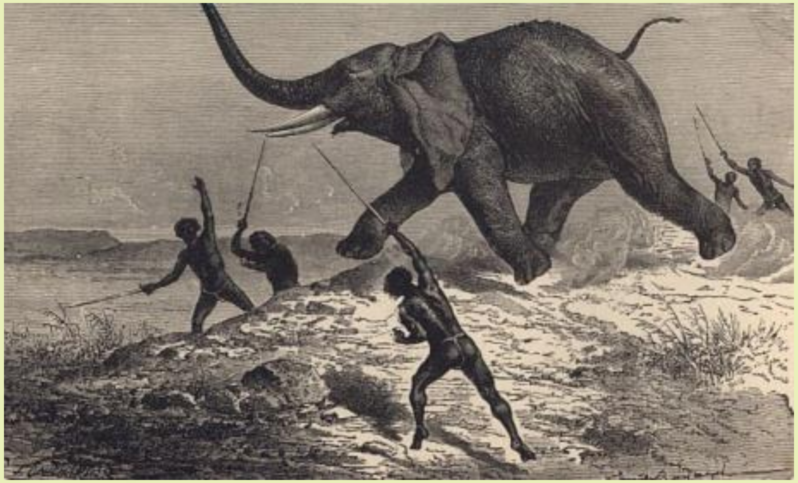




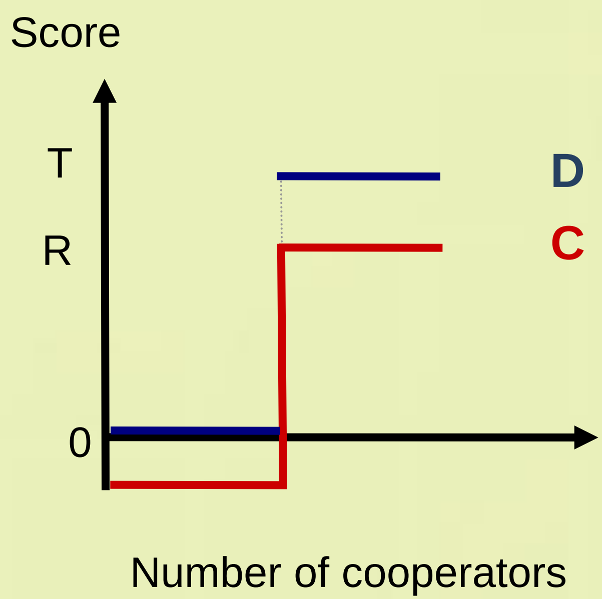
from Hibbing *et al.* (2010)

Non-linear benefit functions

and threshold effects in nature



The Threshold Public Good Game



Threshold value (T)

Threshold Public Good Game

Well–mixed population

Group size (*N*)	3
Threshold value (*T*)	2
Cost of cooperation (*C(x)*)	x -axis
Benefit of cooperation (*b*)	1

	partners		
focal	**CC**	**CD**	**DD**
C	*b-c*	*b-c*	*-c*
D	*b*	*0*	*0*

Individual willingness to cooperate (*x*) is a continuous, evolving trait.

$x = 1$ ⟶ *always cooperate*

$x = 0$ ⟶ *always defect*

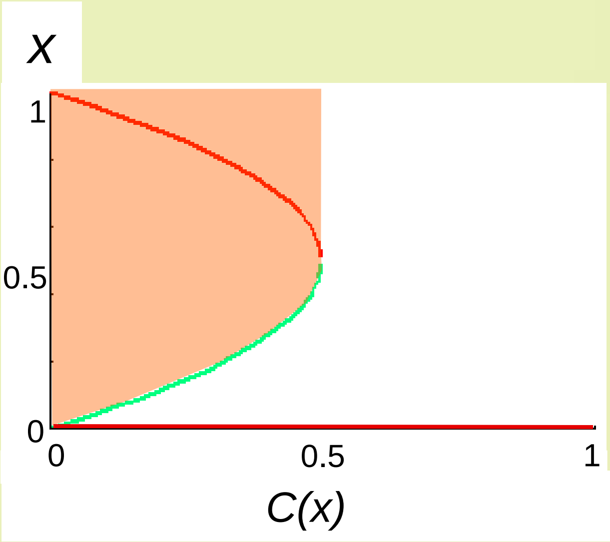
following Bach *et al.* (2006)

Polymorphic equlibria, bifurcation, hysteresis point

C(x) – cost of cooperation

T (threshold value) =2

N (group size) = 3

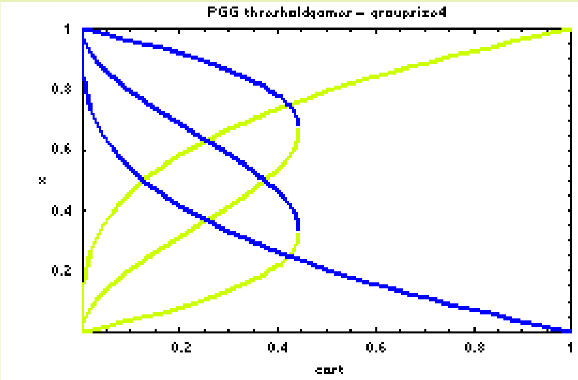


Stable fix points

Instable fix points

Group size

4



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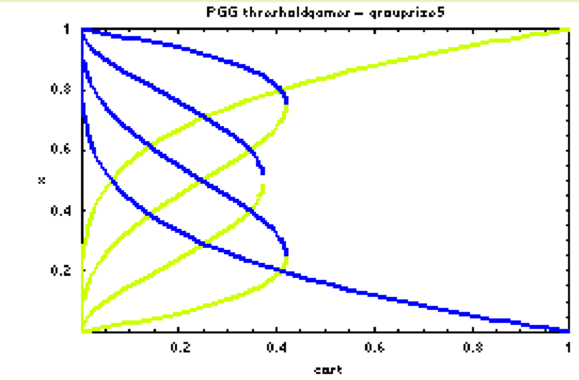

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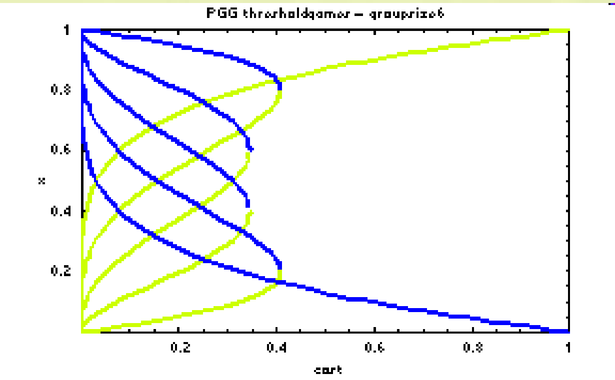

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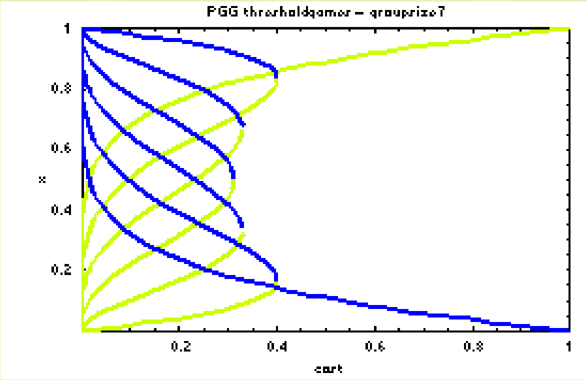

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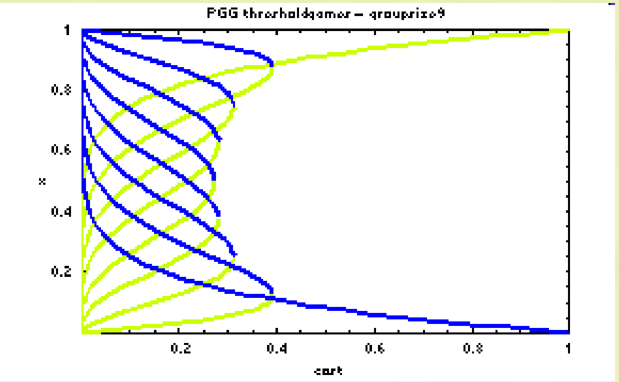
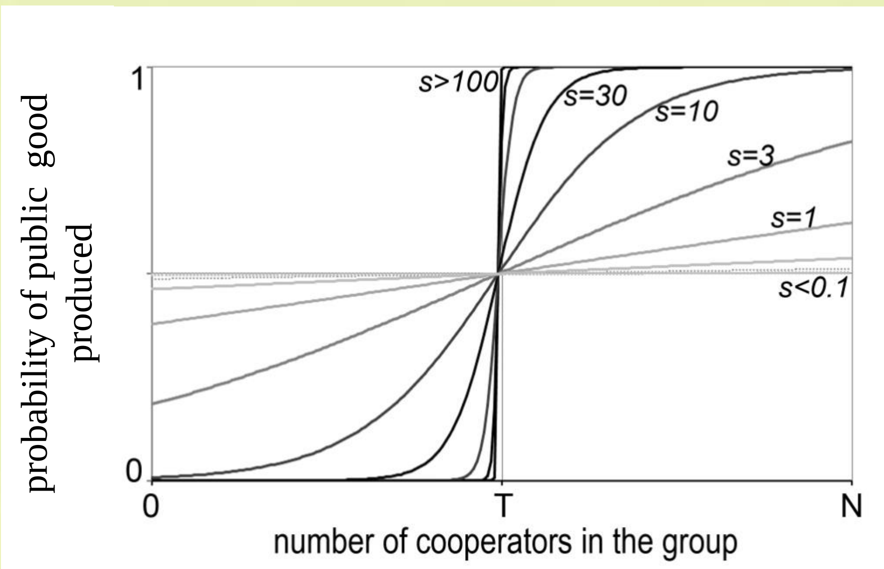
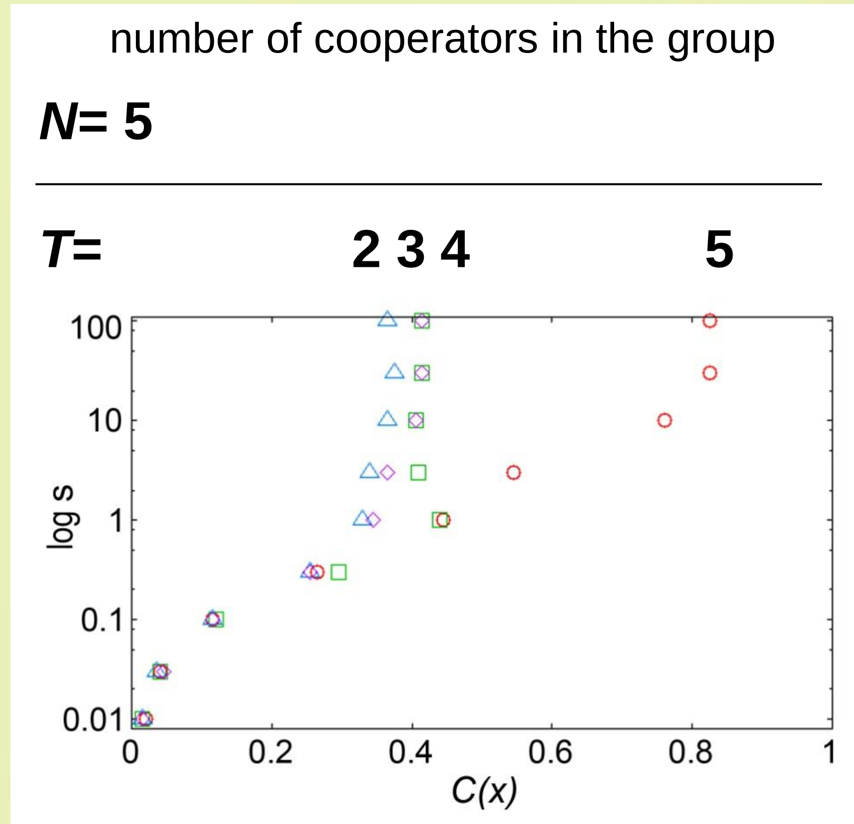


Hysteresis point and the sigmoid return function

$$P(x) = \frac{1}{1 + e^{(n - T) * (- s)}}$$

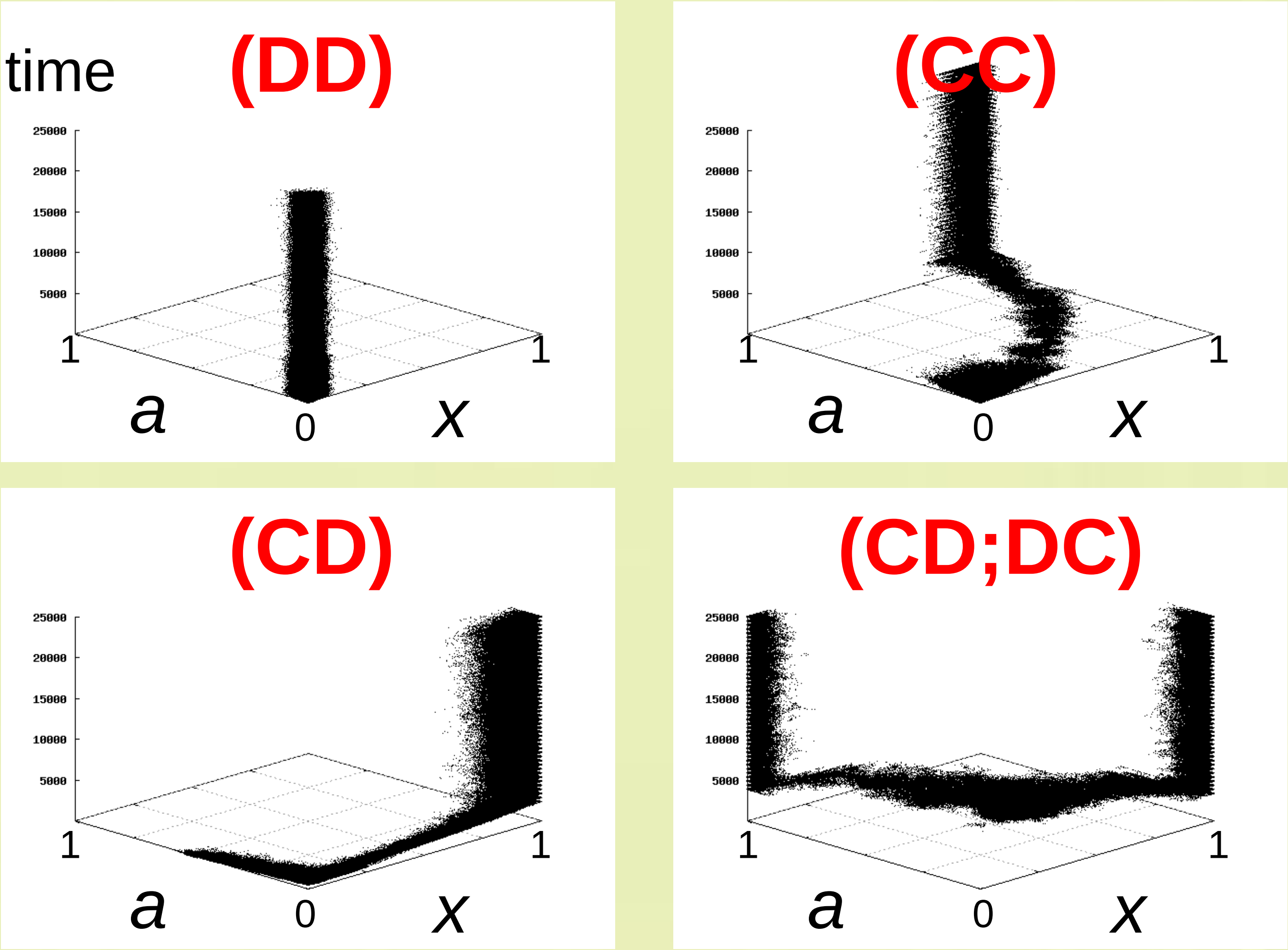
s – steepness





Group cooperation and inter-group conflict

Population structure and multilevel selection



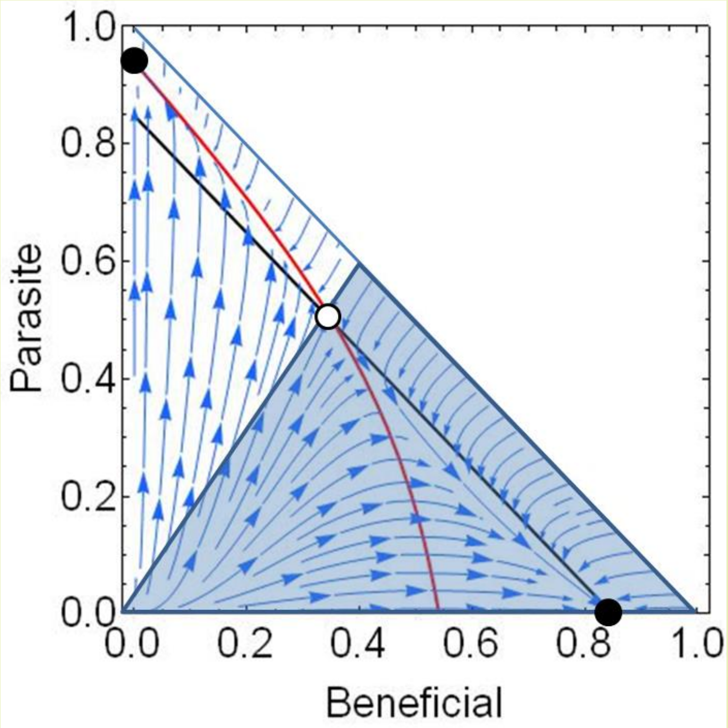
x – willingness to cooperate during cooperative hunting N =5

a – willingness to cooperate during group defence T = 3

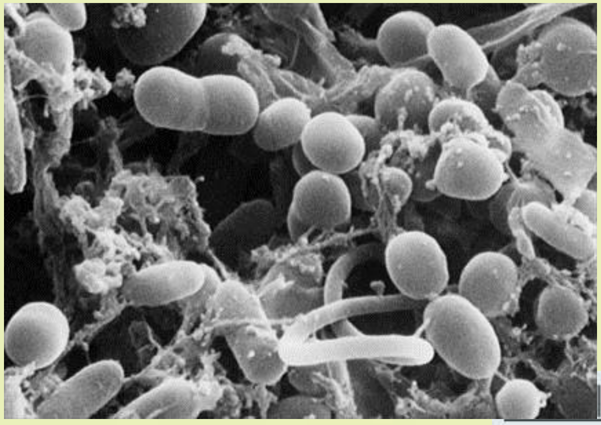
Summary

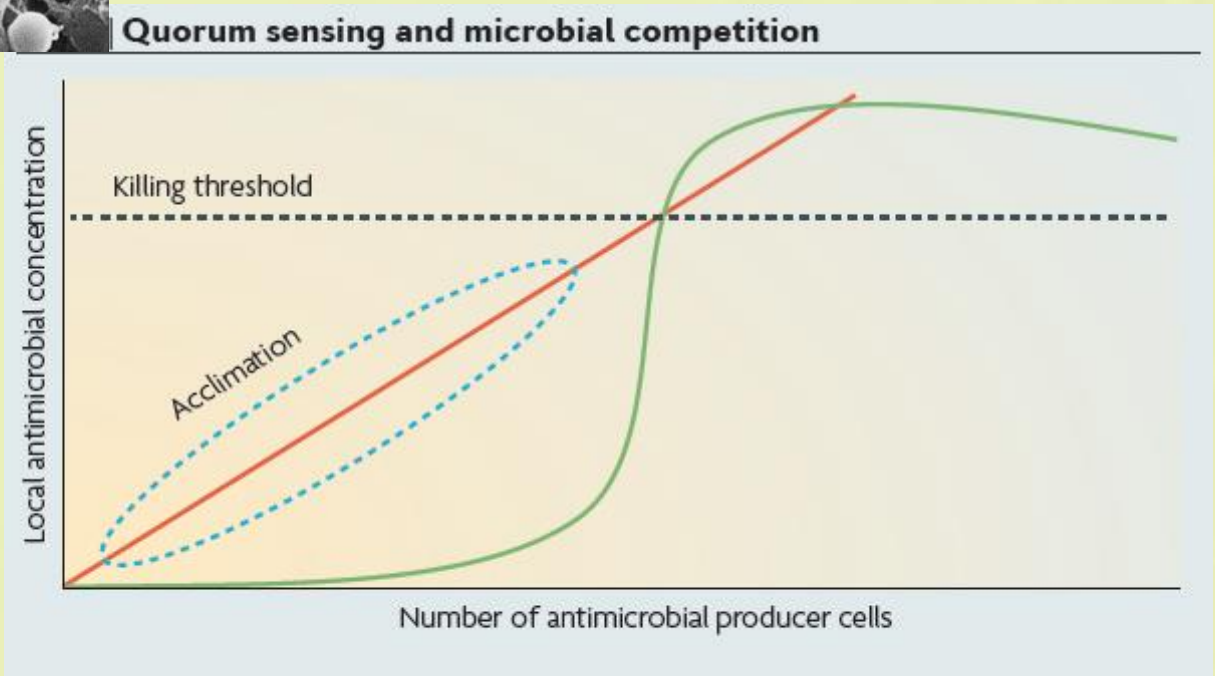
- Non-linear payoff functions are more suited for many phenomena in nature
- Stable polymorphism, coexistence of cooperators and defectors
- Spatial population structure promotes cooperation
- Division of labor in multi-public good games
- Context dependent cooperation (cooperators vs. laggards) assuming intra-group cooperation and inter-group conflict
- Not all non-cooperators are in fact „full” cheaters

Spread of beneficial and parasitic microorganisms in host mediated microbiomes



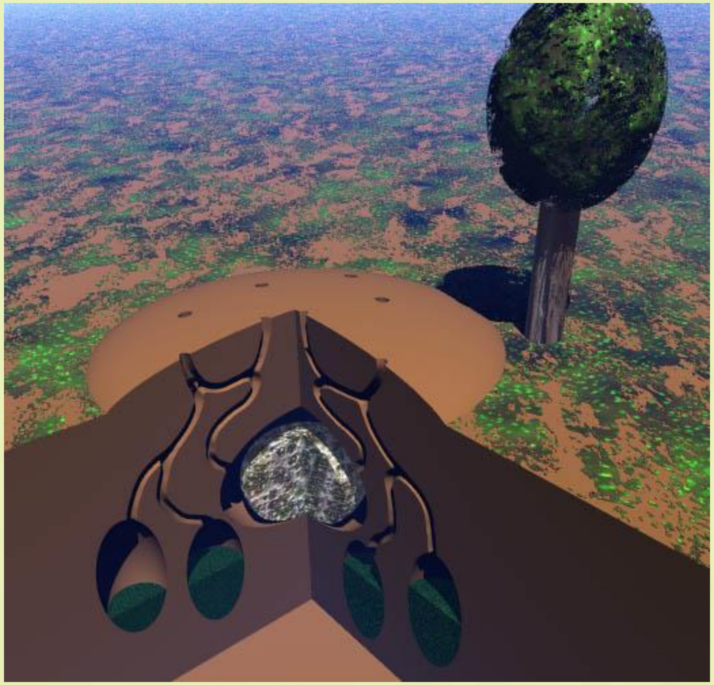
Non-linear dosage-effect function of antibiotics





from Hibbing *et al.* (2010)

Leaf-cutter ant microbiome



Modelling antibiotics producing bacteria

Dynamics of the antibiotics in the environment

$$A_{t+\Delta t}^{\mathrm{Env},i} = A_t^{\mathrm{Env},i} + \left[\frac{D}{\Delta x^2} \left(\sum_{j \in nn} A_t^{\mathrm{Env},j} - 4A_t^{\mathrm{Env},i} \right) + \rho_{\mathrm{pr}/\tau} - \mu^i A_t^{\mathrm{Env},i} + \delta^i A_t^{\mathrm{Int},i} - \phi A_t^{\mathrm{Env},i} \right] \Delta t$$

Intracellular dynamics of the antibiotics

$$A_{t+\Delta t}^{\mathrm{Int},i} = A_t^{\mathrm{Int},i} + \left[\mu^i A_t^{\mathrm{Env},i} - \delta^i A_t^{\mathrm{Int},i} - \lambda^i A_t^{\mathrm{Int},i} \right] \Delta t$$

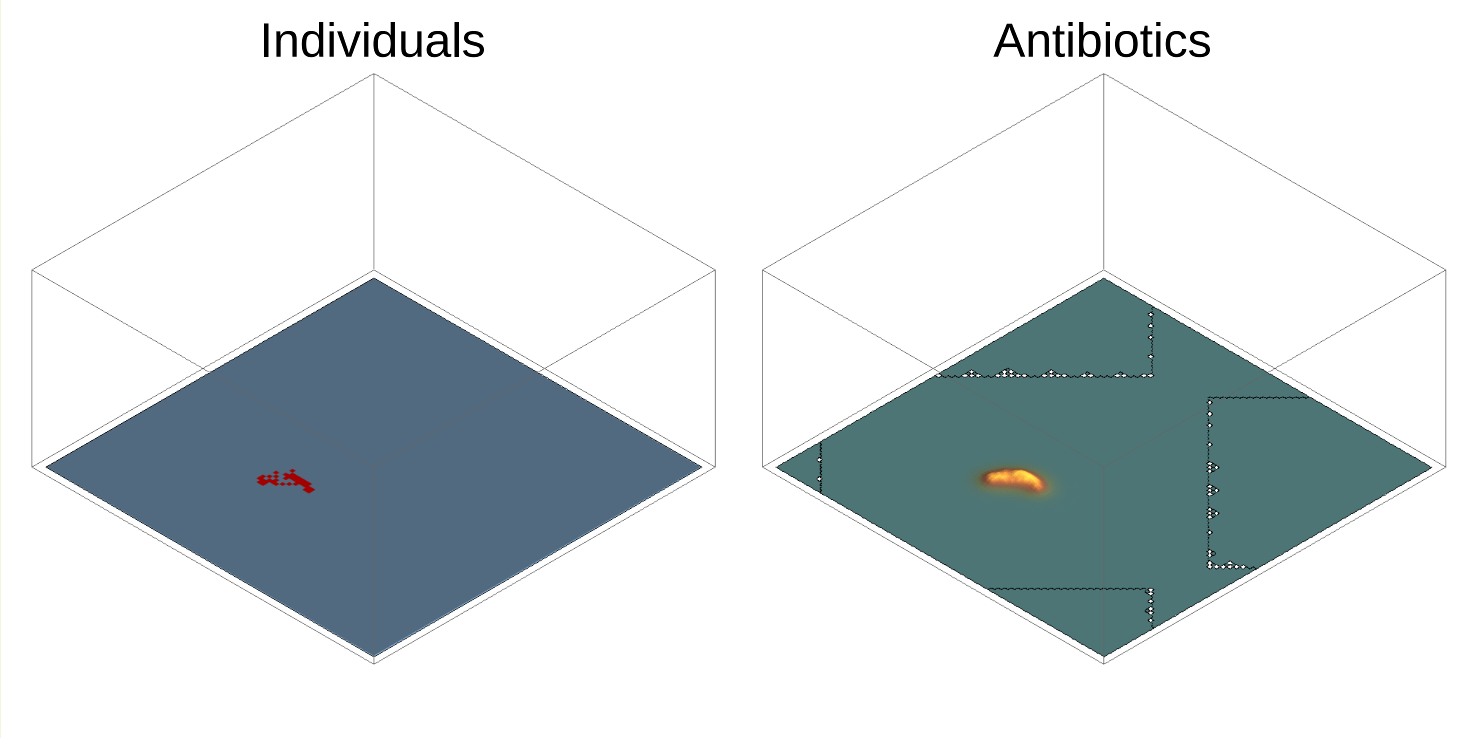
Reproduction rate of the producer (A+R+)

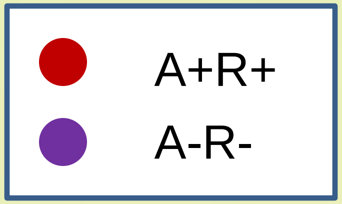
$$r_i^{\mathrm{A+R+}} = r_0^{\mathrm{A+R+}} + r_{\mathrm{pr}}(t) - c_{\mathrm{AR}}$$

Reproduction rate of parasite (A-R-)

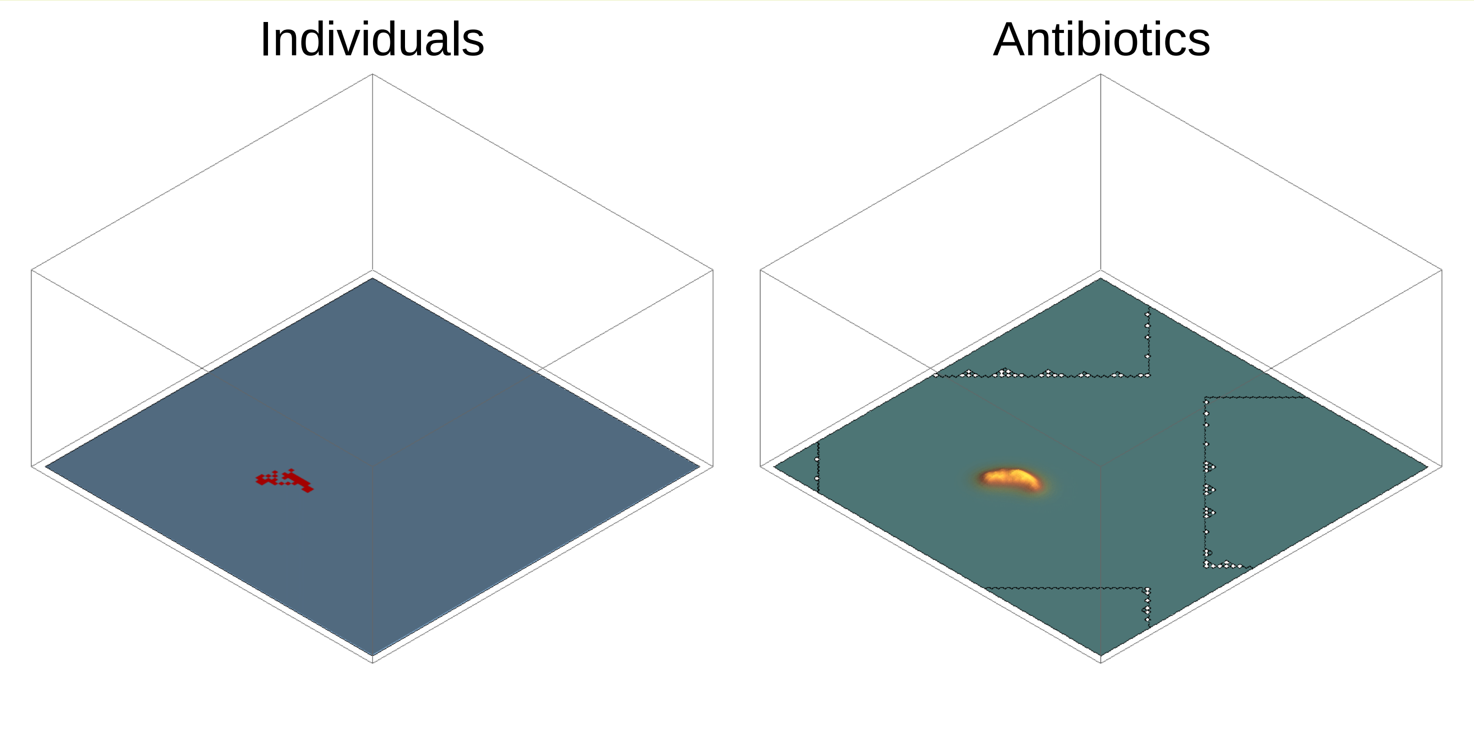
$$r_i^{\mathrm{A\text{-}B\text{-}}} = r_0^{\mathrm{A\text{-}B\text{-}}} + r_{\mathrm{pr}}(t) - \gamma(\alpha, T, A^{\mathrm{Int},i})$$

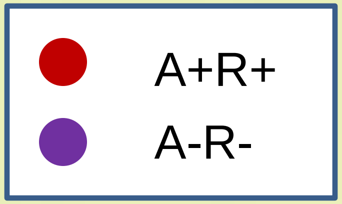
Antibiotics producing vs parasitic bacteria



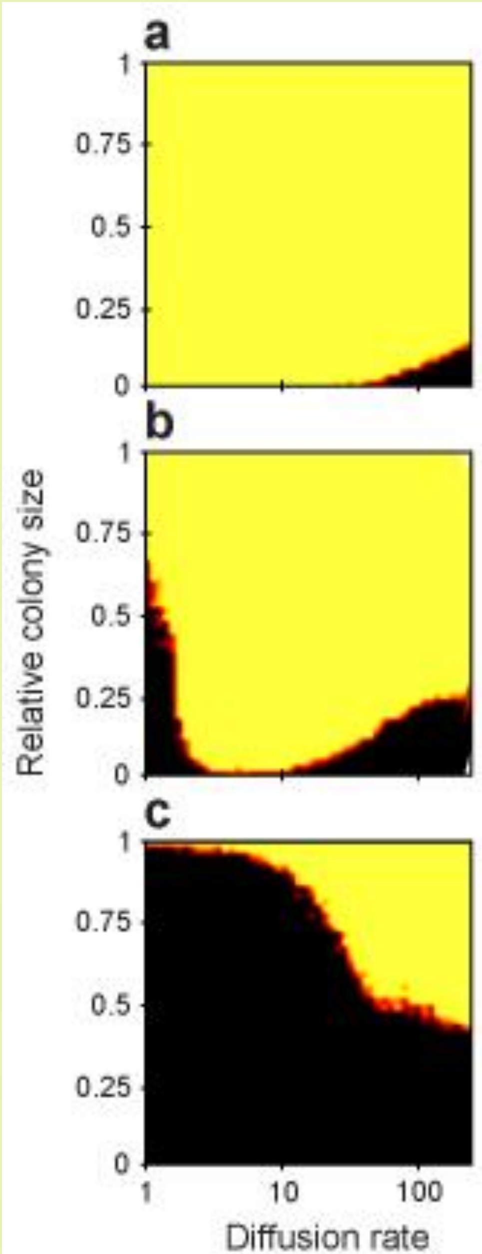


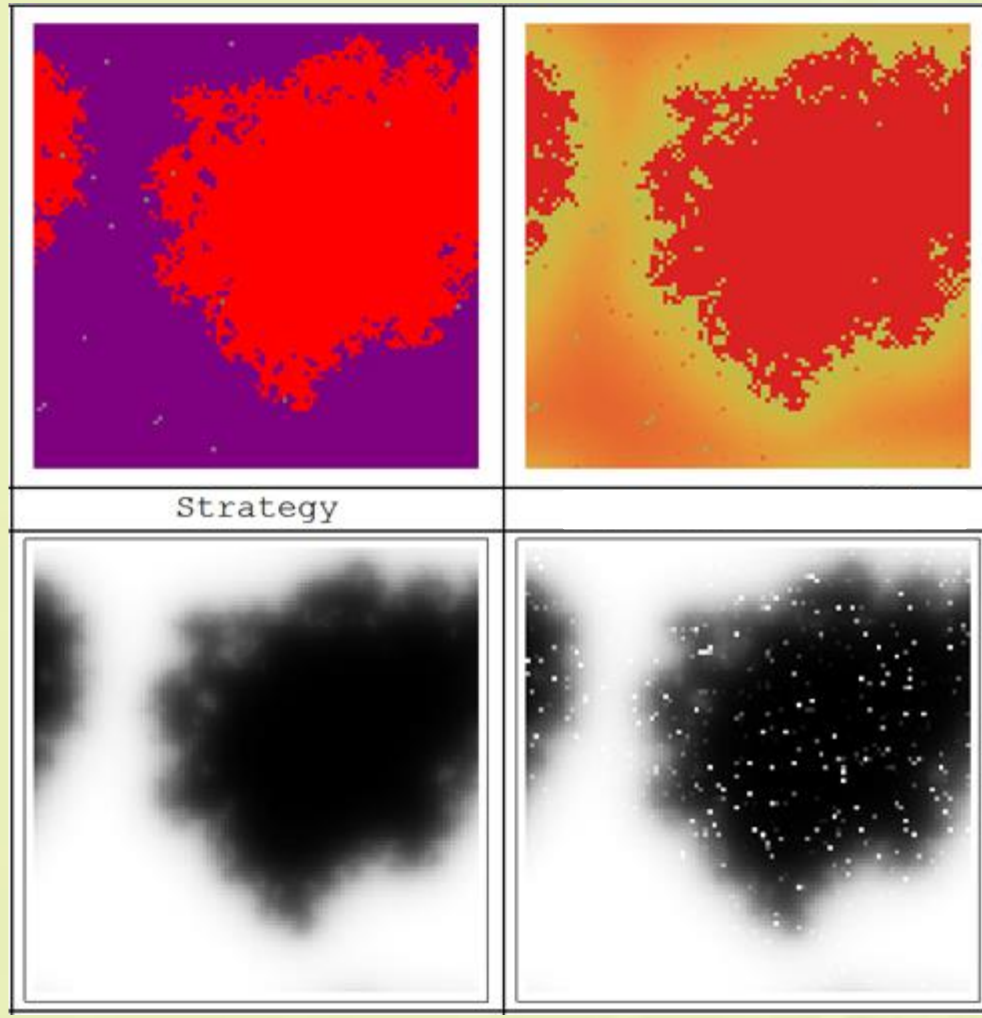
Antibiotics producing vs parasitic bacteria





Antibiotics producing vs parasitic bacteria





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RESEARCH ARTICLE **Open Access**

Beneficial laggards: multilevel selection, cooperative polymorphism and division of labour in Threshold Public Good Games

Gergely Boza[1,3†], Szabolcs Számadó[1,2*†]

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PLOS COMPUTATIONAL BIOLOGY

Strategy Diversity Stabilizes Mutualism through Investment Cycles, Phase Polymorphism, and Spatial Bubbles

Gergely Boza[1,2,3*], Ádám Kun[1,3,4], István Scheuring[5], Ulf Dieckmann[1]

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Thank you for your attention !

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