Introducing physical constraints in models of social and biological evolution

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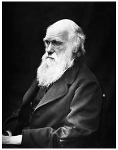
Historical introduction: Towards evolutionary game theory.

Darwin



Natural Selection

Wallace

Natural Selection

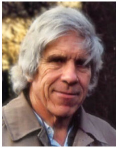
Malthus

Limitation of resources

Kropotkin

Mutual Aid

Hamilton

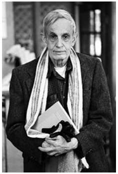


Kin Selection

Price

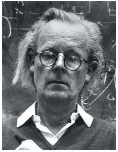
Covariance analysis

Nash



Game Theory

Maynard-Smith



Evolutionary game theory

The importance of cooperation: Evolutionary transitions.

Cooperation between lower-level structural units has been proposed to give rise to **higher order structures**, thus being cooperation a fundamental feature of **the major transitions in evolution**[1].

Transition from	*to*
Replicating molecules	"Populations" of molecules in compartments.
Independent replicators	Chromosomes.
RNA as gene and enzyme	DNA and proteins (genetic code).
Prokaryotes	Eukaryotes
Asexual clones	Sexual populations.
Protists	Multicellular organisms (animals, plants, fungi).
Solitary individuals	Colonies (non-reproductive castes).
Primate societies	Human societies (language, sociocultural evolution)

[1] J. Maynard-Smith & E. Szathmáry (1995). The Major Transitions in Evolution. New York: Oxford University Press.

What is cooperation?

What is cooperation?

Cooperation is the action or process of **working together** to the same end.

What is cooperation?

"**Cooperation**[1] **is an outcome** that -despite potential relative costs to the individual- is **"good"** in some appropriate sense for the members of a group, and whose achievement **requires collective action.**"

[1] Dugatkin, A. (1997). Cooperation among Animals: An Evolutionary Perspective. New York: Oxford University Press.

Cooperation in virus.

Phage Phi-6

Cheaters: Parasitize not only the host, but resources of other viruses.

Figure: Bacteriophages attached to a bacterial cell. Wikipedia

Cooperation in bacteria.

Pseudomonas Aeruginosa Siderophore production. Quorum sensing attached. Cheaters, non-producers of QS signals and/or siderophores.

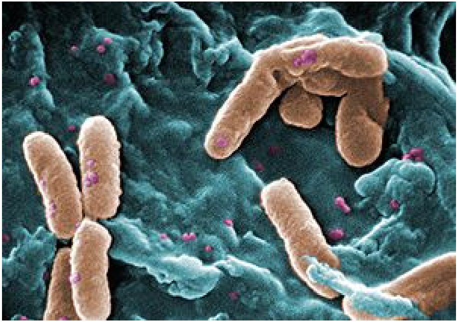


Figure: Electron micrograph of Pseudomonas Aeruginosa. Wikipedia

Cooperation in animals.

Cooperation for hunting

Figure: Lions hunting. Wikipedia

Cooperation in animals.

Defensive cooperation

Figure: Herd of buffalos. Wikipedia

Cooperation in humans.

Tower construction

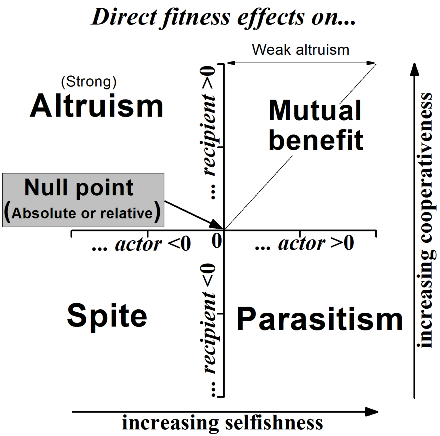
Figure: De Toren van Babel, Pieter Brueghel the Elder, 1563. Kunsthistorisches Museum, Vienna. Wikipedia

The essence of cooperation.

Two main features:

- **Groups of cooperators perform better** than groups including non-cooperators in some appropriate sense.
- It is **more beneficial to interact with cooperative individuals** than with non-cooperative ones.

Modelling cooperation for direct interactions



[1]Requejo-Martínez, R.J., Evolutionary Game Theory and the Tower of Babel of Cooperation. Phys. of Life Rev. (submitted)

The faces of cooperation.

- **Altruism**, pay c, give b; **increases common goods.**
- **Pacific free-rider**, **maintain common goods.**
- **Parasitism**, pay c, steal b; **decreases common goods.**

Prisoner's Dilemma:

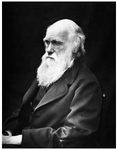
(a)	C	D
C (altruist)	$b_a - c_a$	$-c_a$
D (free-rider)	b_a	0

(1)

Tragedy of the commons, decrease in social goods due to the **evolutionary advantage of defecting strategies**.

Two questions on the evolution of cooperation.

Darwin



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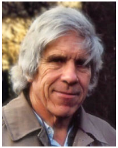

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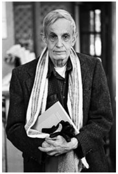

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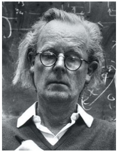


Evolutionary game theory

Two questions on the evolution of cooperation

Evolutionary game theory (replicator equation, stochastic models), does not include explicitly the influence of resources on the evolution of cooperation.

Consumption of common goods.

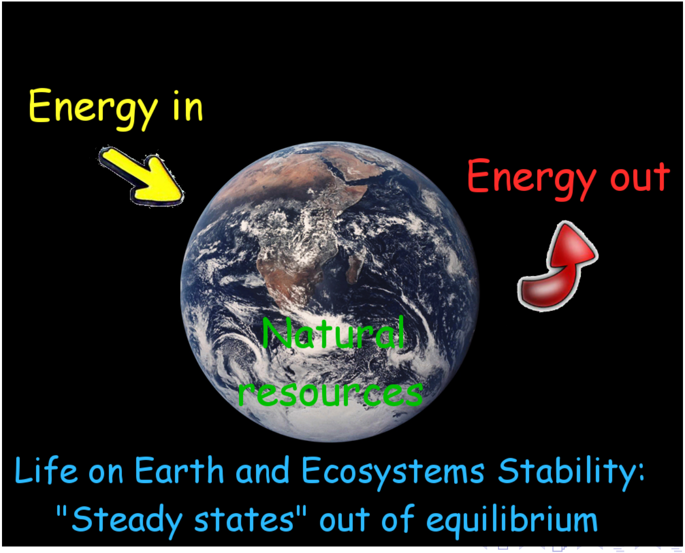
- How does the limited amount of resources influence the evolution of cooperative individuals?

Destruction of common goods

- How do destructive behaviours influence the evolution of altruism?

2. A world of finite resources

A world of finite resources.



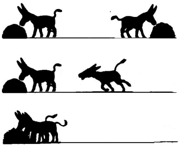
Towards a thermodynamic evolutionary model.

How do energetic constraints influence the evolution of cooperation?

- **Macroscale** - Resource influx and consumption (absorption and dissipation).
- **Mesoscale** - Internal dynamics: Interactions + natural selection.
- **Does the limited amount of resources allow for the evolution of cooperation?**

A model of interactions and evolution including resources[1].

- Individuals: Unconditional cooperators and defectors.
- Resources “equally” distributed among individuals (E_0).
- Reproduction (asexual) when internal resources above E_s.
- Defectors dissipate E_c resources to parasitize E_r from others.
- Random interactions. Random deaths, probability f per unit time.
- **Interactions determine a Prisoner's Dilemma whenever individuals have enough resources.**
- Lack of resources: $E_c \to pE_c$, $E_r \to E'_r$.



[1]R.J. Requejo and J. Camacho. Coexistence of cooperation and defection in well-mixed populations mediated by limiting resources. Phys. Rev. Lett. 108 (2012).

An analytic approach?

Resource dynamics:

$$\frac{dE^C}{dt} = N_C[E_0 - f\overline{E}^C - pE_r'(1-\rho)] \tag{2}$$

$$\frac{dE^D}{dt} = N_D[E_0 - f\overline{E}^D - pE_c + pE_r'\rho] \tag{3}$$

If there exists a coexistence equilibrium:

$$p(E_r' - E_c) = f[\overline{E}^D - \overline{E}^C] \tag{4}$$

Modified replicator equation:

$$\frac{d\rho}{dt} = -a\Delta E'\rho(1-\rho) \tag{5}$$

$\Delta E'$ non-linear function dependent on resources.

An analytic approach?

- Necessary to know the **distribution of resources**. Not a trivial problem.
- Analogy with physics of the **black body**, knowledge of the Planck equation for energy radiation.
- First approach: Simplifying assumptions and testing the results with computer simulations.

An analytic approach?

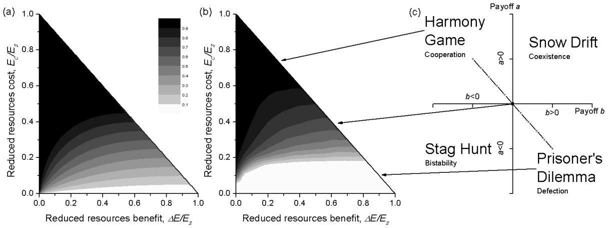
Simplifying assumptions:

- Many interactions per lifetime.
- Homogeneous distribution of resources.
- Linear relationship between parasitized resources and fraction of cooperators (feedback).

$$\rho = \frac{E_c}{E_r - E_r^2/2E_s}. \tag{6}$$

Defection and exhaustion of resources.

(a) “Heuristic” approach, (b) agent-based simulations, (c) games diagram.



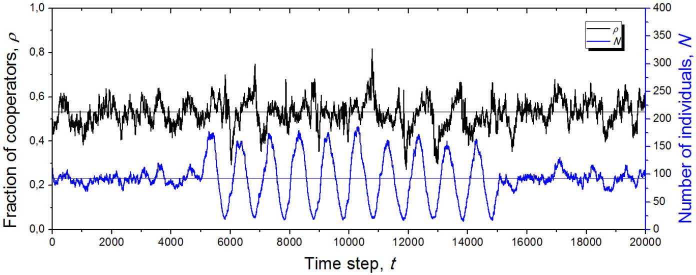
New result in EGT: Self-organizing process leading to neutral coexistence[1].

$$\frac{d\rho}{dt} = -a\Delta E'\rho(1-\rho) \qquad (7)$$

[1]R.J. Requejo and J. Camacho. Coexistence of cooperation and defection in well-mixed populations mediated by limiting resources. Phys. Rev. Lett. 108 (2012).

Defection and exhaustion of resources.

Coexistence robust to variable resource influxes even for small population sizes.

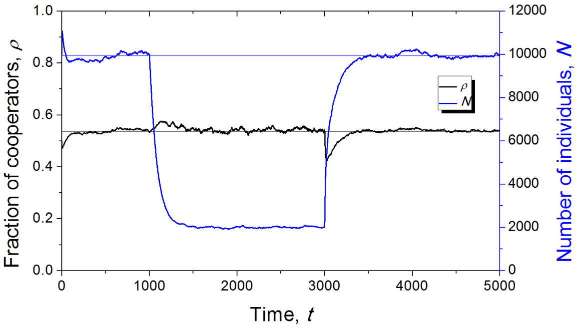


$N = 100$ individuals.

[1] R.J. Requejo and J. Camacho. Coexistence of cooperation and defection in well-mixed populations mediated by limiting resources. Phys. Rev. Lett. 108 (2012).

Defection and exhaustion of resources.

Sudden increases in resource influx promote defection.



[1] R.J. Requejo and J. Camacho. Coexistence of cooperation and defection in well-mixed populations mediated by limiting resources. Phys. Rev. Lett. 108 (2012).

Simplified analytical models.

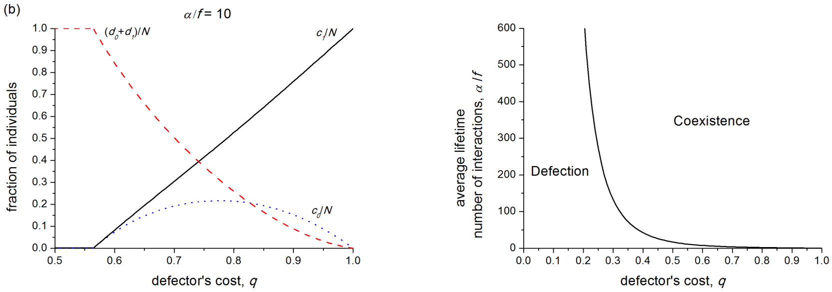
Simplification:

- Only two possible states for internal resources: 1 or 0.
- Defectors act at rate α and dissipate resources with probability q.
- Random deaths with probability f.
- Two adimensional parameters determine the population composition, q and α/f (number of interactions in a lifetime).

[1] R.J. Requejo and J. Camacho. Physical Review E 85, 066112 (2012).
R.J. Requejo and J. Camacho. Physical Review E 87, 022819 (2013).

Simplified analytical models.

Model 1: Phase transition leading to coexistence.



[1] R.J. Requejo and J. Camacho. Physical Review E 85, 066112 (2012).
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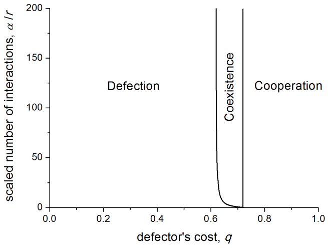
Simplified analytical models.

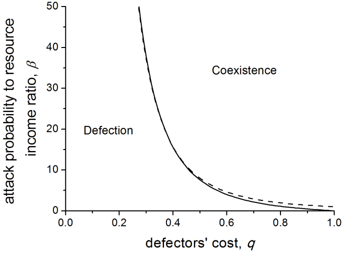
Modelo 2: Variable population size

- Population size dependent resource portions.
- Dissipation or resources (r).
- Deaths when resources below 0.



Modelo 3: Constant population size

- Constant resource portion γ.
- Adjusted deaths to match births.
- Parameter $\beta = \alpha/\gamma$



[1] R.J. Requejo and J. Camacho. Physical Review E 85, 066112 (2012).
R.J. Requejo and J. Camacho. Physical Review E 87, 022819 (2013).

Summary of the results.

Well-mixed populations, strategies determining a PD.

- **Resources constraining reproduction → Internal self-organizing process leading to neutral coexistence**. New result in EGT.
- **Constant population size → Resource-flux dependent phase transition to coexistence**.

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- R.J. Requejo and J. Camacho. Journal of Theoretical Biology 272, 35–41 (2011).
- R.J. Requejo and J. Camacho. Physical Review Letters 108, 038701 (2012).
- R.J. Requejo and J. Camacho. Physical Review E 85, 066112 (2012).
- R.J. Requejo and J. Camacho. Physical Review E 87, 022819 (2013).
- R.J. Requejo. Physics of Life Reviews (submitted).

3. Destruction as source of regeneration

The Joker effect.

Figure: Heath Ledger as the Joker. Wikipedia

Common enemies and danger. Individual point of view.

The appearance of **common enemies triggers cooperation**

- in animal species (alarm calls, defensive aggrupations, ...)
- as well as in humans (coalitions of rival parties, ...)



Figure: (left) Politician as Joker and (center) guppies and (right) the princess bride photogram. Wikipedia

Defectors need cooperators to survive.

Miths and history, a statistical point of view.

- **Religion miths**: Initial cooperation between humans, subsequent defection and Gods wrath destroying the selfish population to give rise to a renewed society.
- **History**: Same behaviour, but destruction product of humans themselves (wars, revolutions, ...). Same for politheistic religions between gods.

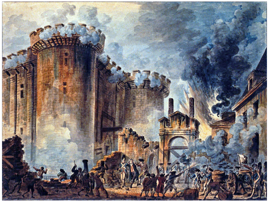




Figure: (left) "The Deluge" by Dor, (center) the storming of the Bastille, French revolution (right) Shiva, deity of creation, destruction and regeneration of Hinduism. Wikipedia

Nature: Cooperation, defection, destruction and cooperation, a statistical view.

- Bacterial warfare: Same dynamical behaviour as before, but unconscious and in a much shorter scale.

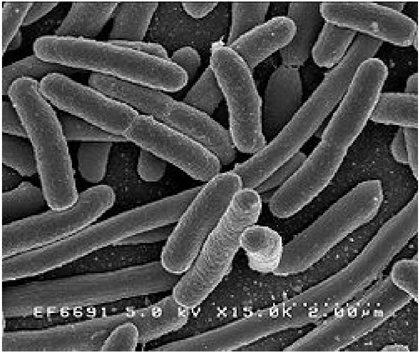


Figure: (left) Escherichia Coli. Wikipedia

A public goods game with Jokers.

Group of n interacting players.

- **Cooperators** $\rightarrow$ **Pay a cost** $c = 1$ and **yield a benefit** r to be distributed among all participants.
- **Defectors** $\rightarrow$ Do not pay the cost but **enjoy the benefits**.
- **Jokers** $\rightarrow$ Do not play the game and create a **damage** $-d < 0$ to the public good.

Fitness $\rightarrow f_i = 1 - s + sP_i$

$P_i \rightarrow$ mean payoff of individuals after playing many times in randomly formed groups.
$s \rightarrow$ Selection strenght.

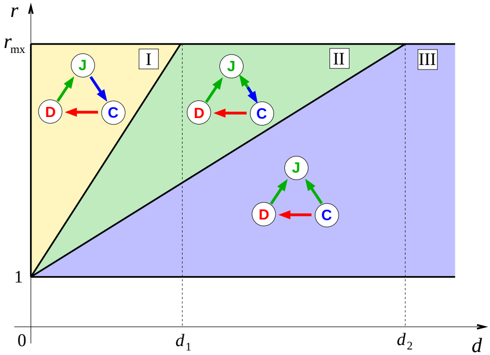
Tragedy of the commons in infinite populations $1 < r < n$

Cooperation, defection, destruction and again cooperation.

I. **Rock-paper-scissors cycle:** $r > 1 + d(n-1)$.

II. **Joker-cooperator bistability**: $1 + d/(M-1) < r < 1 + (n-1)d$.

III. **Joker invasion**: $r < 1 + d/(M-1)$. (M =population size)



[1]A. Arenas, J. Camacho, J.A. Cuesta and R.J. Requejo. J. Theor. Biol. 279, 113-119 (2011).

Cycles in infinite populations.

Replicator dynamics ($s = 1$):

$$\frac{dx}{dt} = x(P_{\mathrm{C}} - \bar{P}) + \mu(1 - 3x),$$
$$\frac{dy}{dt} = y(P_{\mathrm{D}} - \bar{P}) + \mu(1 - 3y),\qquad (8)$$
$$\frac{dz}{dt} = z(P_{\mathrm{J}} - \bar{P}) + \mu(1 - 3z),$$

[1] A. Arenas, J. Camacho, J.A. Cuesta and R.J. Requejo. J. Theor. Biol. 279, 113-119 (2011).

Cycles in infinite populations.

I. **Rock-paper-scissors cycle:** $r > 1 + d(n-1)$. A single cooperator gets a positive payoff in spite of the damage inflicted by $n-1$ jokers.

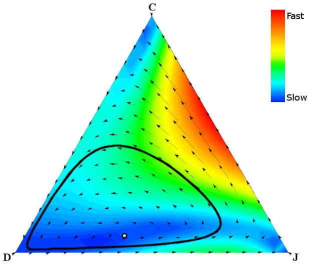


Figure: $n = 5$, $r = 3$, $d = 0.4$, $s = 1$ and $\mu = 0.005$; $n > r > 1 + d(n-1)$

[1] A. Arenas, J. Camacho, J.A. Cuesta and R.J. Requejo. J. Theor. Biol. 279, 113-119 (2011).

Cycles in finite populations.

Cycles happen in populations of any size; 100 individuals below.

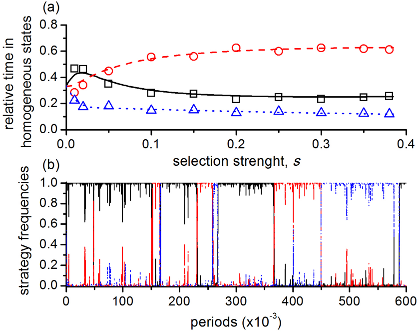


Figure: Modified Moran process, $n = 5$, $r = 3$, $d = 0.4$ and $\mu = 0.005$; (b) $s = 0.05$.

[1]R.J. Requejo, J. Camacho, J.A. Cuesta and A. Arenas. Phys. Rev. E 86, 026105 (2012)

Cycles in finite populations. Stochastic dynamics.

Transition probability $T(m', j'|m, j)$ from a population with composition (m, j) to another one with composition (m', j').

Master equation:

$$\mathbf{\Pi}(t+1) = \mathbf{T}\,\mathbf{\Pi}(t). \tag{9}$$

Transition matrix: $\mathbf{T} = \mathbf{T_0} + \mathbf{T_1}$

$\mathbf{T_0}$ is the transition matrix in the absence of mutations. $\mathbf{T_1}$ includes the effect of mutations.

[1] R.J. Requejo, J. Camacho, J.A. Cuesta and A. Arenas. Phys. Rev. E 86, 026105 (2012)

Stochastic dynamics in finite populations.

Proportional imitation

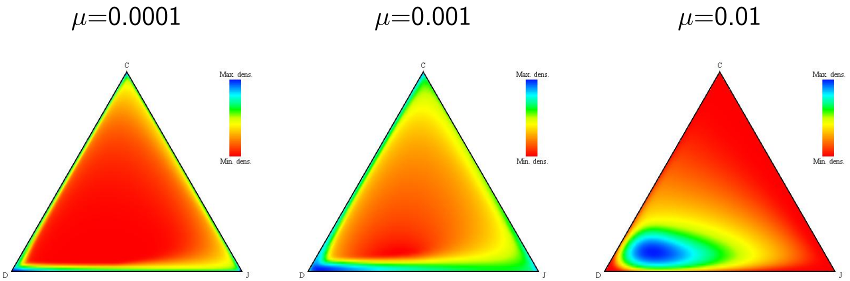


Figure: Probability of finding the system in each state. A logarithmic scale has been used in the plots. Parameters: $n = 5, r = 3, d = 0.4, s = 1$

[1]R.J. Requejo, J. Camacho, J.A. Cuesta and A. Arenas. Phys. Rev. E 86, 026105 (2012)

External agents. Darwin vs. Kropotkin.

- Kropotkin → Darwinian struggle for existence harder in environments that support life than **in harsh environments**, as Siberia, where **mutual aid is promoted.**
- **The Joker may be regarded as external damage.** Natural disasters (or gods wrath), antibiotics introduced in the system, ...
- **Accurate predictions of the behaviour of the system** may allow for new treatments to control infectious deseases and cancer, reducing the risk of re-infection.

Summary of the results

The finiteness of resources promotes cooperation in well-mixed populations of unconditional cooperators and defectors playing an a-priori prisoner's dilemma.

- **Self-organising process that tunes the interaction structure to neutral.**
- Resource mediated phase transitions.

Indiscriminate destruction promotes cycles of cooperation, defection and destruction.

- **First example of robust limit cycles with unconditional strategies in the public goods game.**

Collaborators

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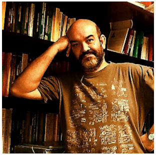

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¡Hasta la próxima!

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