Tutorial

Concepts and recent results in coevolutionary games

Hendrik Richter

HTWK Leipzig University of Applied Sciences

Faculty of Electrical Engineering & Information Technology

Leipzig, Germany

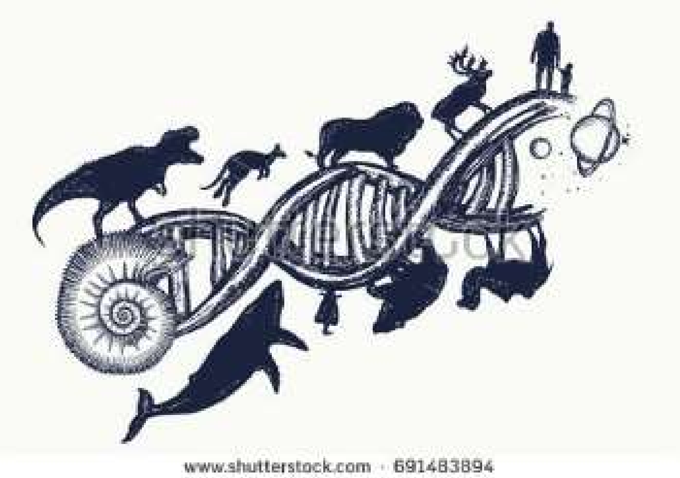
Content

- Concepts and mathematical models of evolutionary/coevolutionary games
  - Players and strategies
  - Interaction networks: Evolutionary graph theory
  - Strategies and configurations
- Games and co-evolutionary dynamics
  - Parameterization of the payoff matrix and payoff space
  - Social dilemma games: prisoner's dilemma (PD), snowdrift (SD), stag-hunt (SH), harmony (H) games
  - Nash equilibria and evolutionary stable strategies (ESS)
  - Dilemma strength and universal scaling
  - Frequency dependence
  - Fixation properties: fixation probabilities and fixation times
  - Structure coefficients
- Computational issues
  - Replicator dynamics
  - Models for updating strategies and interaction networks
  - Landscape view on coevolutionary games
- Open questions and research topics

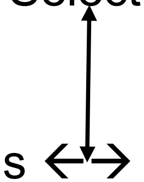
Evolutionary and Coevolutionary Games

- **What is evolution?**

Biologically:
Evolution acts on population of individuals



Building blocks of evolution



Mutation → Differences in Fitness → Selection → Reproduction

Competitions ↔ Cooperation

Richard Dawkins
The selfish gene (1976)
“It can be selfish to be altruistic”
OR “It can be altruistic to be selfish…”

Images: https://daybreaksdevotions.wordpress.com/
https://phys.org/

Evolutionary and Coevolutionary Games

- **Why evolutionary and coevolutionary games?**

Address a long-standing and fundamental problem in Darwinian evolution

Two seemingly contradictory observations:

One: Population of reproducing individuals → phenotypic differences → selective pressure → survival and reproduction of best adapted (a.k.a. fittest) → competition

Two: Wide-spread cooperative and even altruistic behavior between individuals (and groups of individuals and even species)

Q: How can selection favor fitter individual while cooperation levels fitness?

(Co)-evolutionary games: mathematical models for discussing

Q: Whether, when and under what circumstances is cooperation more advantageous than competition?

Evolutionary and Coevolutionary Games

Evolutionary games

Population of players $I = \left(I_1, I_2, \ldots, I_N\right)$

Each player I_i may use one of two strategies $C_i \; D_i$

Cooperating
Defecting

Player I_i interacting with player I_j
gives payoff according to a payoff matrix

$$\begin{array}{c|cc} & C_j & D_j \\ \hline C_i & R & S \\ D_i & T & P \end{array}$$

Reward
Temptation
Sucker payoff
Punishment

Numerical values and order yield
particular examples of social dilemma games

Snowdrift game (SD) $T > R > S > P$
Prisoner's dilemma game (PD) $T > R > P > S$
Stag hunt (trust dilemma) (SH) $R > T \geq P > S$

Evolutionary and Coevolutionary Games

- **Evolutionary game dynamics**

We need three entities to specify an evolutionary game

→ Who-gets-what: **Payoff matrix** defining the payoff for each strategy

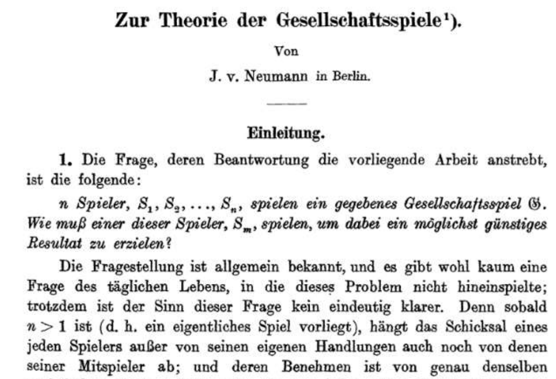
→ Who-plays-whom: **Interaction network** defining with whom any player interacts (for more than 2 players)

→ Who-plays-what: **Strategy vector** defining the strategy of each player → **Configuration** of the game

Vary all three of these entities

Evolutionary and Coevolutionary Games: Some early history

(On the Theory of Games) Math. Ann. 100: 295–320 (1928)



Zur Theorie der Gesellschaftsspiele[1]).

Von

J. v. Neumann in Berlin.

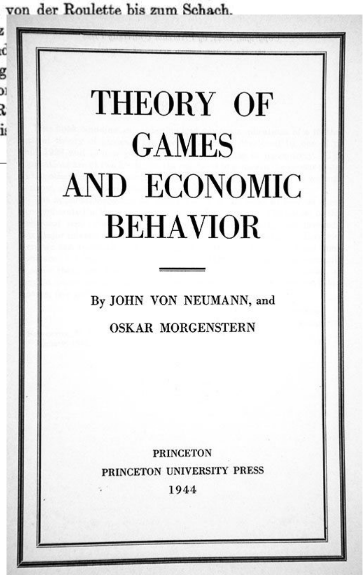
Einleitung.

1. Die Frage, deren Beantwortung die vorliegende Arbeit anstrebt, ist die folgende:

n Spieler, $S_1, S_2, \ldots, S_n$, spielen ein gegebenes Gesellschaftsspiel $\mathfrak{G}$. Wie muß einer dieser Spieler, S_m, spielen, um dabei ein möglichst günstiges Resultat zu erzielen?

Die Fragestellung ist allgemein bekannt, und es gibt wohl kaum eine Frage des täglichen Lebens, in die dieses Problem nicht hineinspielte; trotzdem ist der Sinn dieser Frage kein eindeutig klarer. Denn sobald $n > 1$ ist (d. h. ein eigentliches Spiel vorliegt), hängt das Schicksal eines jeden Spielers außer von seinen eigenen Handlungen auch noch von denen seiner Mitspieler ab; und deren Benehmen ist von genau denselben egoistischen Motiven beherrscht, die wir beim ersten Spieler bestimmen möchten. Man fühlt, daß ein gewisser Zirkel im Wesen der Sache liegt.

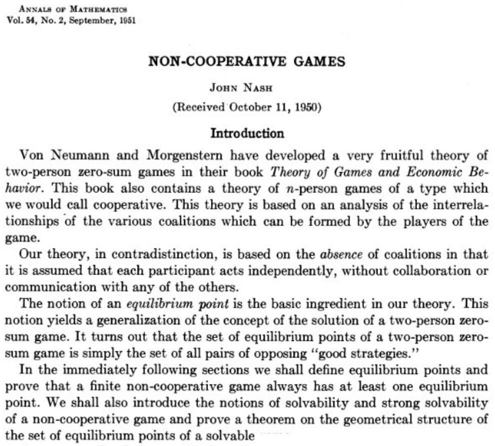
Wir müssen also versuchen, zu einer klaren Fragestellung zu kommen. Was ist zunächst ein Gesellschaftsspiel? Es fallen unter diesen Begriff sehr viele, recht verschiedenartige Dinge: von der Roulette bis zum Schach, vom Bakkarat bis zum Bridge liegen ganz
melbegriffes „Gesellschaftsspiel" vor. Und
ein Ereignis, mit gegebenen äußeren Beding
(den absolut freien Willen der letzteren vo
angesehen werden, wenn man seine R
handelnden Personen betrachtet[2]). Was i
aller dieser Dinge?



THEORY OF
GAMES
AND ECONOMIC
BEHAVIOR

By JOHN VON NEUMANN, and
OSKAR MORGENSTERN

PRINCETON
PRINCETON UNIVERSITY PRESS
1944



Annals of Mathematics
Vol. 54, No. 2, September, 1951

NON-COOPERATIVE GAMES

John Nash

(Received October 11, 1950)

Introduction

Von Neumann and Morgenstern have developed a very fruitful theory of two-person zero-sum games in their book *Theory of Games and Economic Behavior*. This book also contains a theory of n-person games of a type which we would call cooperative. This theory is based on an analysis of the interrelationships of the various coalitions which can be formed by the players of the game.

Our theory, in contradistinction, is based on the *absence* of coalitions in that it is assumed that each participant acts independently, without collaboration or communication with any of the others.

The notion of an *equilibrium point* is the basic ingredient in our theory. This notion yields a generalization of the concept of the solution of a two-person zero-sum game. It turns out that the set of equilibrium points of a two-person zero-sum game is simply the set of all pairs of opposing "good strategies."

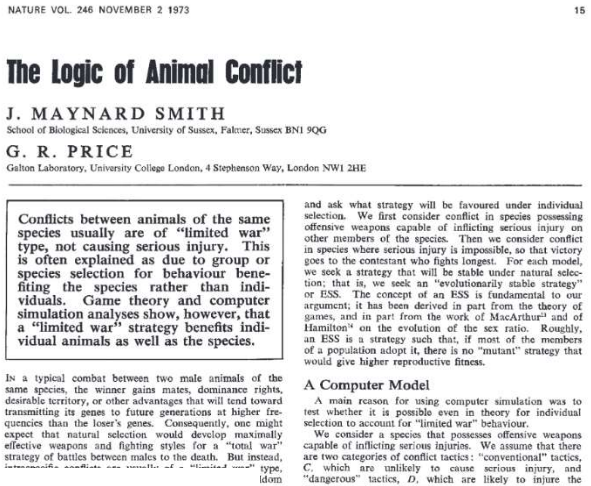
In the immediately following sections we shall define equilibrium points and prove that a finite non-cooperative game always has at least one equilibrium point. We shall also introduce the notions of solvability and strong solvability of a non-cooperative game and prove a theorem on the geometrical structure of the set of equilibrium points of a solvable

As an example of the application of
simplified three person poker game.

Formal Definitions

In this section we define the basic conc
terminology and notation. Important de
indicating the concept defined. The non-c
than explicit, below.

Finite Game:



NATURE VOL. 246 NOVEMBER 2 1973 15

The Logic of Animal Conflict

J. MAYNARD SMITH
School of Biological Sciences, University of Sussex, Falmer, Sussex BN1 9QG
G. R. PRICE
Galton Laboratory, University College London, 4 Stephenson Way, London NW1 2HE

Conflicts between animals of the same species usually are of "limited war" type, not causing serious injury. This is often explained as due to group or species selection for behaviour benefiting the species rather than individuals. Game theory and computer simulation analyses show, however, that a "limited war" strategy benefits individual animals as well as the species.

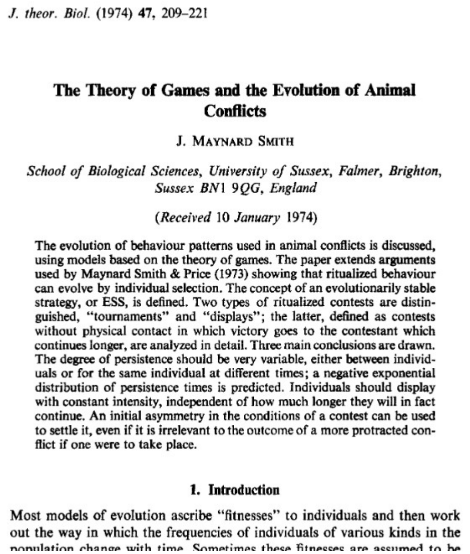
In a typical combat between two male animals of the same species, the winner gains mates, dominance rights, desirable territory, or other advantages that will tend toward transmitting its genes to future generations at higher frequencies than the loser's genes. Consequently, one might expect that natural selection would develop maximally effective weapons and fighting styles for a "total war" strategy of battles between males to the death. But instead,

and ask what strategy will be favoured under individual selection. We first consider conflict in species possessing offensive weapons capable of inflicting serious injury on other members of the species. Then we consider conflict in species where serious injury is impossible, so that victory goes to the contestant who fights longest. For each model, we seek a strategy that will be stable under natural selection; that is, we seek an "evolutionarily stable strategy" or ESS. The concept of an ESS is fundamental to our argument; it has been derived in part from the theory of games, and in part from the work of MacArthur[13] and of Hamilton[14] on the evolution of the sex ratio. Roughly, an ESS is a strategy such that, if most of the members of a population adopt it, there is no "mutant" strategy that would give higher reproductive fitness.

A Computer Model

A main reason for using computer simulation was to test whether it is possible even in theory for individual selection to account for "limited war" behaviour.

We consider a species that possesses offensive weapons capable of inflicting serious injuries. We assume that there are two categories of conflict tactics: "conventional" tactics, *C*, which are unlikely to cause serious injury, and "dangerous" tactics, *D*, which are likely to injure the opponent seriously if they are employed for long. (Thus in the snake example, wrestling involves *C* tactics and use of fangs would be *D* tactics. In many species, *C* tactics



J. theor. Biol. (1974) **47**, 209–221

The Theory of Games and the Evolution of Animal Conflicts

J. Maynard Smith

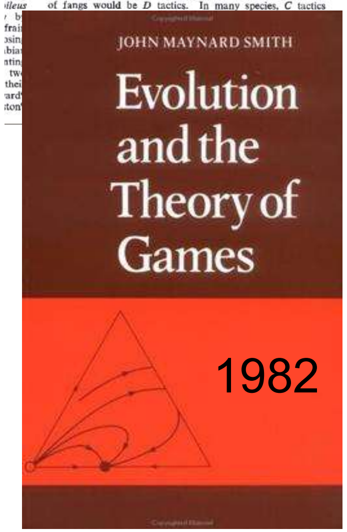
*School of Biological Sciences, University of Sussex, Falmer, Brighton, Sussex BN*1 *9QG, England*

(*Received* 10 *January* 1974)

The evolution of behaviour patterns used in animal conflicts is discussed, using models based on the theory of games. The paper extends arguments used by Maynard Smith & Price (1973) showing that ritualized behaviour can evolve by individual selection. The concept of an evolutionarily stable strategy, or ESS, is defined. Two types of ritualized contests are distinguished, "tournaments" and "displays"; the latter, defined as contests without physical contact in which victory goes to the contestant which continues longer, are analyzed in detail. Three main conclusions are drawn. The degree of persistence should be very variable, either between individuals or for the same individual at different times; a negative exponential distribution of persistence times is predicted. Individuals should display with constant intensity, independent of how much longer they will in fact continue. An initial asymmetry in the conditions of a contest can be used to settle it, even if it is irrelevant to the outcome of a more protracted conflict if one were to take place.

1. Introduction

Most models of evolution ascribe "fitnesses" to individuals and then work out the way in which the frequencies of individuals of various kinds in the



1982

Evolutionary game dynamics: What are we interested in?

Hierarchy of game dynamics:

Game playing → each player
uses its strategy
plays scheduled coplayers
receives payoff p_i

Convert payoff to fitness $f_i = 1 + \delta p_i$

Intensity of selection δ
(= influence of a single game on total)

Weak selection $\delta << 1$

Play again → no game dynamics

A players changes strategy → evolutionary game dynamics

Players change interaction network → coevolutionary game dynamics

Evolutionary game dynamics: What are we interested in?

Hierarchy of asymptotic game dynamics

- Which players has how much payoff (or fitness) after a certain time?
Iterated games, repeated games → Player deliberately selects strategy
(for instance Tit-for-Tat, Win-stay-Lose-switch)
- Classical evolutionary game theory, 1980s (John Maynard Smith, Robert Axelrod, William D. Hamilton)

- How are strategies distributed over players after a certain time?
- What is the probability that all players settle on one strategy?
- Is there a fixation of strategy?
- Under what circumstance is the fixated strategy ‘Cooperation’?
- How to promote the emergence of ‘Cooperation’ or ‘Evolution of Cooperation’?
1990s and ongoing (Martin Nowak, Chris Hauert, Hisashi Ohtsuki)

- How does the structure of the interaction network interfere with fixation?
- Network structure is object to evolve → Current topic (and of the future…)

Evolutionary game dynamics

→ Who-gets-what: **Payoff matrix** defining the payoff for each strategy

→ Who-plays-whom: **Interaction network** defining with whom any player interacts (for more than 2 players)

→ Who-plays-what: **Strategy vector** defining the strategy of each player → **Configuration** of the game

Evolutionary and Coevolutionary Games: Payoff matrix

- **2-strategy game → 4D parameter space**

$$\begin{array}{c|cc} & C_j & D_j \\ \hline C_i & R & S \\ D_i & T & P \end{array}$$

- **2-player game**

Classification of 2-strategy-2-player games with respect to game-theoretical difference

How many Nash equilibria there are? What is the type of the Nash equilibria?
Nash equilibria (NE) and evolutionary stable strategies (ESS)

NE = best response to another player's strategy (no other strategy yields higher payoff

ESS = strategy that cannot be invaded by any alternative (yet initially rare) strategy

NE not necessarily equal ESS

Evolutionary and Coevolutionary Games: Payoff matrix

- **2-strategy game → 4D parameter space**

$$\begin{array}{cc} & \begin{array}{cc} C_j & D_j \end{array} \\ \begin{array}{c} C_i \\ D_i \end{array} & \begin{pmatrix} R & S \\ T & P \end{pmatrix} \end{array}$$

- **2-player game**

Numerical values and order yield particular examples of social dilemma games

$$(R, S, T, P)$$

Snowdrift game (SD) (also chicken or hawk-dove) $T > R > S > P$

Prisoner’s dilemma game (PD) $T > R > P > S$

Stag hunt game (SH) $R > T \geq P > S$

Harmony game (H) $R > S \geq T > P$

2-player games: Snowdrift game (also chicken or hawk-dove)

- **2-strategy game → 4D parameter space**

$$\begin{tikzcd} & C_j & D_j \\ C_i & R \arrow[r] & S \arrow[d] \\ D_i & T \arrow[u] & P \end{tikzcd}$$

- **Snowdrift game (also chicken or hawk dove)**

The game: A snowdrift blocks a road. Two drivers are on opposite sides of the block. Each can either start shovel away snow to clear the path or wait. Highest reward: Let opponent do all work. Then: Do it together. Then: Do it yourself. Last: Both do nothing.

Image: James Pollard (1792-1867), „A mail coach in snow drift“
www.artwarefineart.com

Order of parameter $T > R > S > P$

Nash equilibria: three polymorphic equilibria
→ either players choose opposite strategies (cooperate vs. defect, or defect vs. cooperate) or
→ randomly switch between cooperating and defecting

2-player games: Prisoner’s dilemma game

- **2-strategy game → 4D parameter space**

$$\begin{tikzcd} & C_j & D_j \\ C_i & R \arrow[dr] & S \\ D_i & T \arrow[u] & P \arrow[u] \end{tikzcd}$$

- **Prisoner’s dilemma**

The game: Two people are arrested. Prosecutor can charge both with small crime but lacks evidence to convince both of larger crimes. Deal to both: Betray the other and go free. Highest reward: Betray, while the other does not. Then: Both not betraying. Then: Both betraying. Last: Not betraying, while the other does.

Image: Ilya Repin (1844-1930) „Arrest of a propagandist“
www.imrussia.org

Order of parameter $T > R > P > S$

Nash equilibria: monomorphic → all players defect

2-player games: Stag hunt game (coordination game, trust dilemma)

- **2-strategy game → 4D parameter space**

$$\begin{tikzcd} & C_j & D_j \\ C_i & R \arrow[d] & S \\ D_i & T \arrow[r] & P \arrow[u] \end{tikzcd}$$

- **Stag hunt (coordination game or trust dilemma)**

The game: (Jean-Jacques Rousseau)
Two people go on a hunt. Each can hunt a stag (together) or a hare (each by himself). Highest reward: Hunt together a stag. Then: Each hunts a hare. Last: Go stag hunting alone.

Image: Frans Snyders (1579-1657) „Deer hunting“, www.wikiart.org

Order of parameter $R > T \geq P > S$

Nash equilibria: two pure Nash equilibria, bi-stable
→ either all players cooperate, or
→ all players defect

2-player games: Harmony game

- **2-strategy game → 4D parameter space**

$$\begin{tikzcd} & C_j & D_j \\ C_i & R \arrow[r] & S \arrow[dl] \\ D_i & T \arrow[r] & P \end{tikzcd}$$

- **Harmony game**

The game: No formal description as no conflict.

Order of parameter $R > S \geq T > P$

Image: Pieter Bruegel (1525-1569) „Preparation of the flower beds“
www.pieter-bruegel-the-elder.org/

Nash equilibria: monomorphic → all players cooperate

2-player games: General remark

- **2-strategy game → 4D parameter space**

$$\begin{array}{ccc} & C_j & D_j \\ C_i & R & S \\ D_i & T & P \end{array}$$

PD	prisoner's dilemma
SD	snow drift (chicken, hawk-dove)
SH	stag hunt
H	harmony

Conflict between individual and group
(what is best for me vs. what is best for group)

Typical 2x2 games (R,S,T,P)
More games with specific

Evolutionary games: More than 2 players

Evolutionary and Coevolutionary Games: Payoff matrix

- **Social dilemmas and Nash equilibria**

$$\begin{array}{ccc} & C_j & D_j \\ C_i & R & S \\ D_i & T & P \end{array}$$

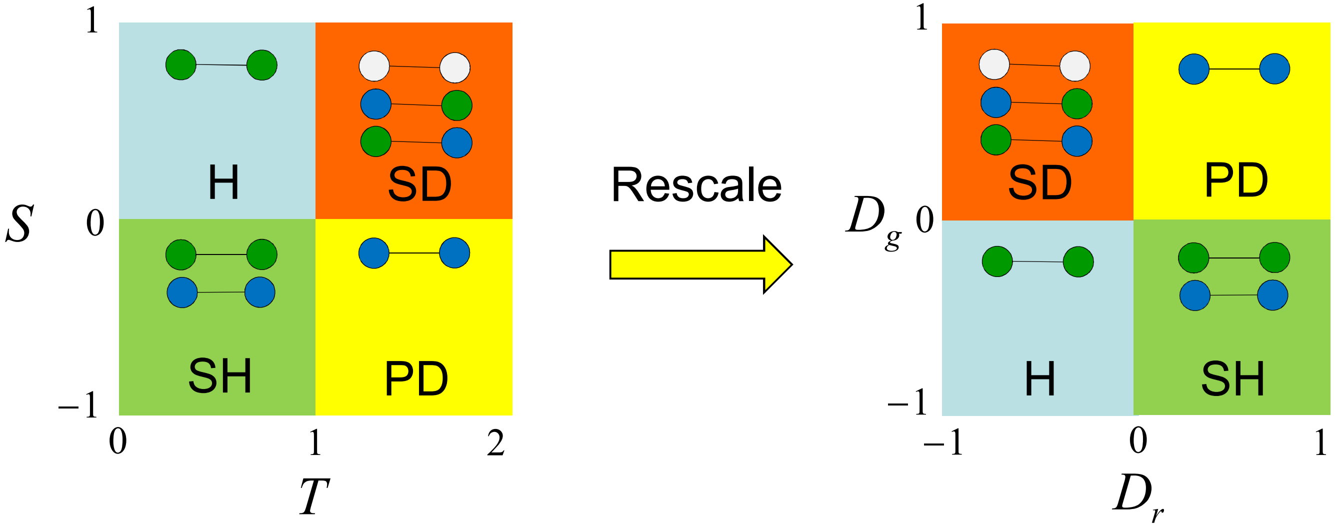
Reward
Temptation
Sucker payoff
Punishment

$$\begin{array}{ccc} & C_j & D_j \\ C_i & R & P-D_r \\ D_i & R+D_g & P \end{array}$$

🟢 Always cooperate

🔵 Always defect

⚪ Mix both



PD	prisoner‘s dilemma
SD	snow drift (chicken, hawk-dove)
SH	stag hunt
H	harmony

<u>Dilemma strength</u>

$D_r = P - S$ risk-averting

$D_g = T - R$ gamble intending

Rescaling of payoff matrices (Wang et al., 2015)

$$\begin{array}{ccc} & C_j & D_j \\ C_i & R & S \\ D_i & T & P \end{array}$$

$$\begin{array}{ccc} & C_j & D_j \\ C_i & R & P-(R-P)v \\ D_i & R+(R-P)u & P \end{array}$$

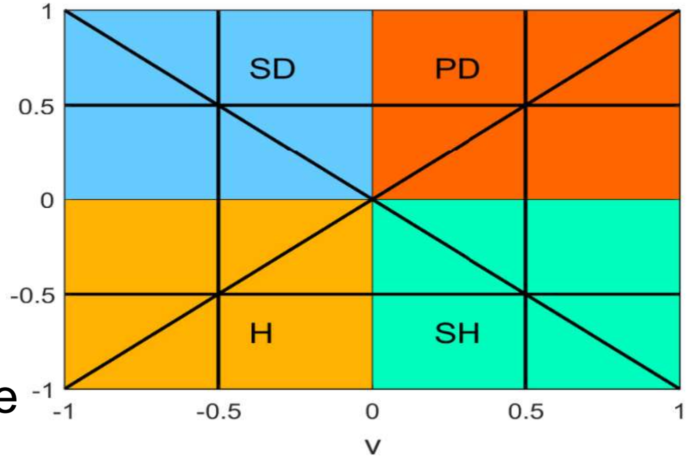
$$u = \frac{T-R}{R-P} \qquad v = \frac{P-S}{R-P} \qquad R > P$$

$$-1 \le \left\{ \begin{matrix} T-R \\ P-S \end{matrix} \right\} \le 1$$

(R,S,T,P) Different orders
Different social dilemmas

$$-1 \le \left\{ \begin{matrix} u \\ v \end{matrix} \right\} \le 1$$

Traversing a 2D parameter space with relevant dilemmas

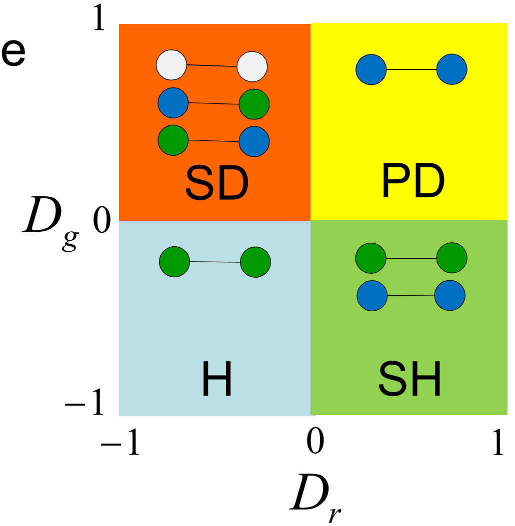


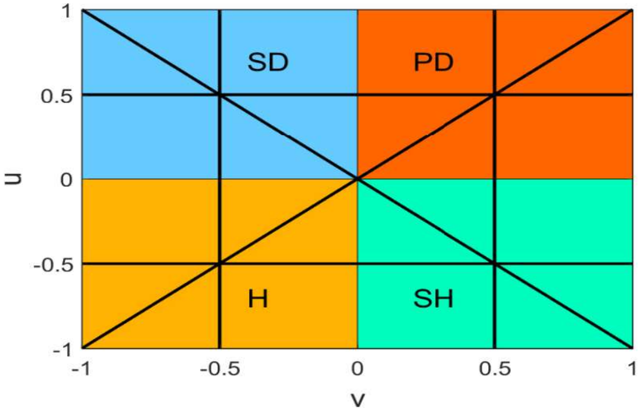
Evolutionary and Coevolutionary Games: Payoff matrix

🟢 Always cooperate

🔵 Always defect

⚪ Mix both





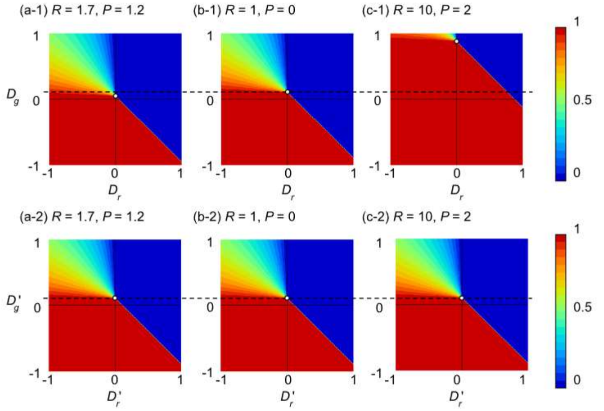


Fig. 4. Equilibrium fraction of cooperators in D_r–D_g (upper panels) and D'_r–D'_g (lower panels) diagrams with direct reciprocity. The parameters are (a) $R = 1.7$, $P = 1.2$, (b) $R = 1$, $P = 0$, and (c) $R = 10$, $P = 2$. In all cases the probability of meeting each other in another round is $w = 0.1$.

Fixation properties do not scale to *R* and *P*

Wang et al. (2015)

Evolutionary and Coevolutionary Games

- **Coevolutionary game dynamics**

For payoff matrix, strategy for each player and interaction network fixed
→ payoff distribution always the same

Make the game dynamic: → update strategies
(evolutionary game)
replication and replicator rules

→ update network of interaction
(coevolutionary game)

Strategy updating: Intensively researched field in evolutionary games

Strategy updating: stochastic process with probabilities depending on fitness (Moran process)

Network models and updating: evolutionary graph theory

Evolutionary game dynamics

→ Who-gets-what: **Payoff matrix** defining the payoff for each strategy

→ Who-plays-whom: **Interaction network** defining with whom any player interacts (for more than 2 players)

→ Who-plays-what: **Strategy vector** defining the strategy of each player → **Configuration** of the game

Evolutionary and Coevolutionary Games: Interaction network

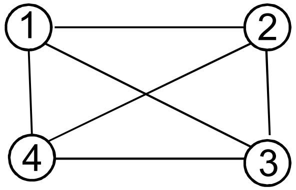
Evolutionary graph theory

Population of N players: who-plays-whom (who is coplayer to whom)
→ Network of interaction

Evolutionary graph theory (Lieberman et al.,2005)
Every player → vertex of a graph
Two players interacting → edge between the player vertices

Two Examples: $N = 4$ players

all playing all others
(but no self-play)

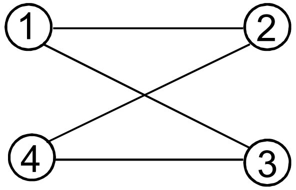


Adjacency matrix

$$A_I = \begin{pmatrix} 0 & 1 & 1 & 1 \\ 1 & 0 & 1 & 1 \\ 1 & 1 & 0 & 1 \\ 1 & 1 & 1 & 0 \end{pmatrix}$$

Complete network of interaction

player 1 vs. (2&3); player 3 vs. (1&4)
player 2 vs. (1&4); player 4 vs. (2&3)

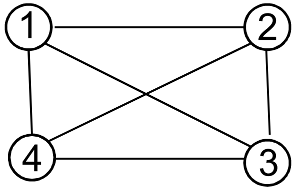


Adjacency matrix

$$A_I = \begin{pmatrix} 0 & 1 & 1 & 0 \\ 1 & 0 & 0 & 1 \\ 1 & 0 & 0 & 1 \\ 0 & 1 & 1 & 0 \end{pmatrix}$$

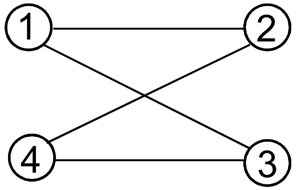
Evolutionary and Coevolutionary Games: Interaction network

Evolutionary graph theory: graph-theoretical concepts and implications



Adjacency matrix

$$A_I = \begin{pmatrix} 0 & 1 & 1 & 1 \\ 1 & 0 & 1 & 1 \\ 1 & 1 & 0 & 1 \\ 1 & 1 & 1 & 0 \end{pmatrix}$$



Adjacency matrix

$$A_I = \begin{pmatrix} 0 & 1 & 1 & 0 \\ 1 & 0 & 0 & 1 \\ 1 & 0 & 0 & 1 \\ 0 & 1 & 1 & 0 \end{pmatrix}$$

Degree of a vertex = number of edges = number of coplayers

Same degree for all vertices = regular graph = number of coplayers same

Adjacency matrix symmetric = undirected graph = players mutually interact

Main diagonal zeros = no self-edges = no self-play

Complete matrix = complete graph = well-mixed game

Structured matrix = regular (or any) graph = structured population

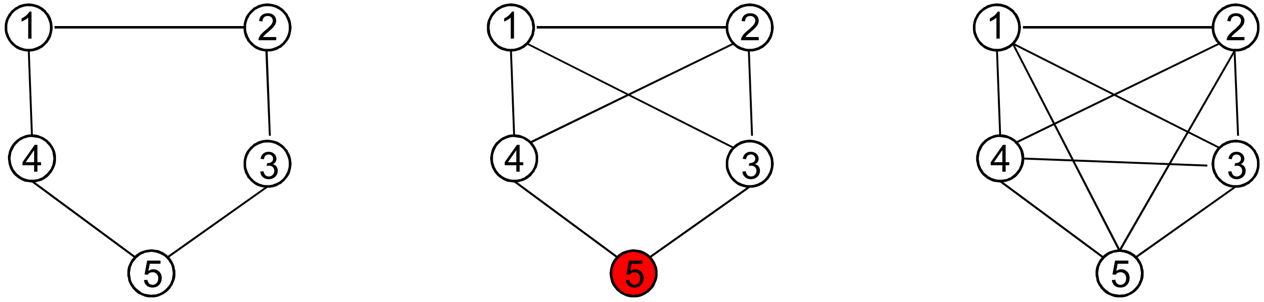
Evolutionary and Coevolutionary Games: Interaction network

- **d-regular graphs on *N* vertices: computational models of interaction networks**

Interaction network → interaction graph → instance of an Erdös-Rényi graph

Any *d*-regular graph on *N* vertices → interaction network with *N* players and *d* coplayer

Any *d*-regular graph on *N* vertices → *dN/2* edges → *dN* even



N=5, d=2 *N=5, d=3* *N=5,d=4*

Numerical experiments with *N* even
Numerical experiments vary over *N* and *d*

Evolutionary and Coevolutionary Games: Interaction network

- **d-regular graphs on *N* vertices: computational models of interaction networks**

Recently, efficient algorithms to generate such graphs (Bayati et al.,2010)
Number of different 2-regular graphs by iteration

$$L_2(N) = (N-1)L_2(N-1) + \frac{(N-2)(N-3)}{2} L_2(N-3) \qquad N \geq 3$$

$$L_2(0) = 1$$

$$L_2(1) = L_2(2) = 0$$

$$L_2(4) = 3$$

$$L_2(6) = 70$$

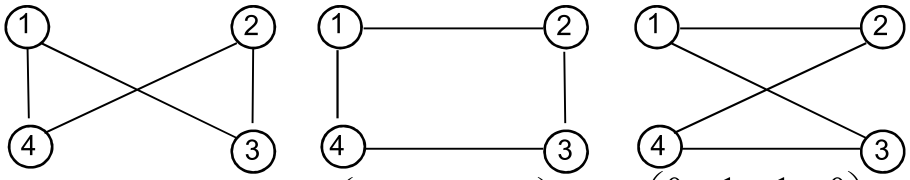
$$L_2(8) = 3507$$

$$L_2(10) = 286884$$

$$L_2(12) = 34944085$$

$$\dots$$

$$L_2(20) \approx 1.4 \cdot 10^{17}$$



$$A_I = \begin{pmatrix} 0 & 0 & 1 & 1 \\ 0 & 0 & 1 & 1 \\ 1 & 1 & 0 & 0 \\ 1 & 1 & 0 & 0 \end{pmatrix} \quad A_I = \begin{pmatrix} 0 & 1 & 0 & 1 \\ 1 & 0 & 1 & 0 \\ 0 & 1 & 0 & 1 \\ 1 & 0 & 1 & 0 \end{pmatrix} \quad A_I = \begin{pmatrix} 0 & 1 & 1 & 0 \\ 1 & 0 & 0 & 1 \\ 1 & 0 & 0 & 1 \\ 0 & 1 & 1 & 0 \end{pmatrix}$$

Evolutionary and Coevolutionary Games: Interaction network

- **d-regular graphs on *N* vertices: computational models of interaction networks**

No formula known to calculate the number of *d*-regular graphs on *N* vertices

Asymptotic approximation for *dN* even and $d = o\left(\sqrt{N}\right)$, Wormald, 1999

$$L_d(N) = \frac{(dN)! \cdot \exp\left(\frac{1-d^2}{4} - \frac{d^3}{12N} + O(d^2/N)\right)}{(dN/2)! \cdot 2^{\frac{dN}{2}} \cdot (d!)^N}$$

Hugh number of different graphs for sufficient large *d* and *N*

$$L_d = O\left(N^N\right), d << N$$

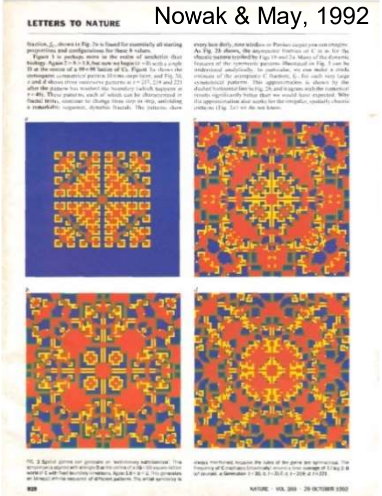
→ Numerical experiments may take into account only a tiny subset

Evolutionary and Coevolutionary Games: Interaction network

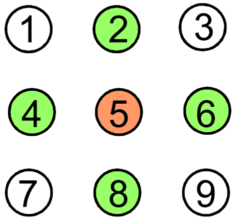
- **Evolutionary graph theory: generalizes spatial games**

  Spatial games on a lattice grid: Coplayers are spatial neighbors (edges overlapping)

  ⓘ player ⓙ coplayer


Nowak & May, 1992

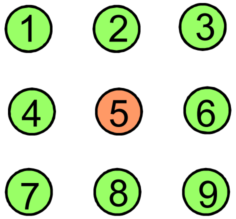
Von Neumann neighborhood



$$A_I = \begin{pmatrix} 0 & 1 & 1 & 1 & 0 & 0 & 1 & 0 & 0 \\ 1 & 0 & 1 & 0 & 1 & 0 & 0 & 1 & 0 \\ 1 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 & 1 & 1 & 1 & 0 & 0 \\ 0 & \textcircled{1} & 0 & \textcircled{1} & 0 & \textcircled{1} & 0 & \textcircled{1} & 0 \\ 0 & 0 & 1 & 1 & 1 & 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 1 & 0 & 0 & 0 & 1 & 1 \\ 0 & 1 & 0 & 0 & 1 & 0 & 1 & 0 & 1 \\ 0 & 0 & 1 & 0 & 0 & 1 & 1 & 1 & 0 \end{pmatrix}$$

4-regular graph over 9 vertices
General: Specific *4*-regular graph on N vertices

Moore neighborhood



$$A_I = \{a_{ij}\}, a_{ij} = 1, a_{ii} = 0$$

Complete graph
→ *well-mixed game*

8-regular graph over 9 vertices
General: Specific *8*-regular graph on N vertices

Evolutionary and Coevolutionary Games

Evolutionary game dynamics

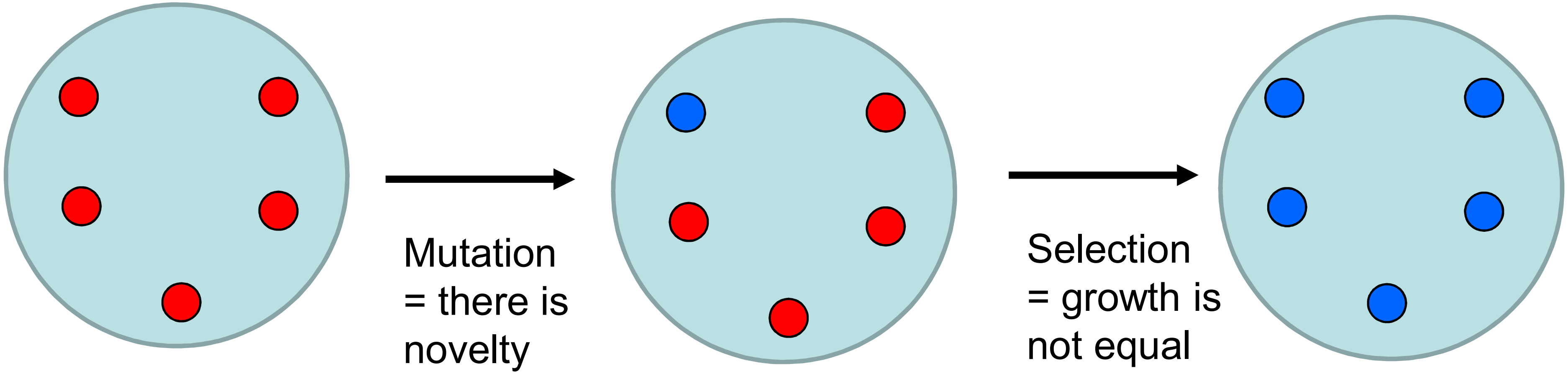
→ Who-gets-what: **Payoff matrix** defining the payoff for each strategy

→ Who-plays-whom: **Interaction network** defining with whom any player interacts (for more than 2 players)

→ Who-plays-what: **Strategy vector** defining the strategy of each player → **Configuration** of the game

Game Dynamics and Fixation Properties: Strategy vector

- **Fundamental elements in evolution of evolutionary games**

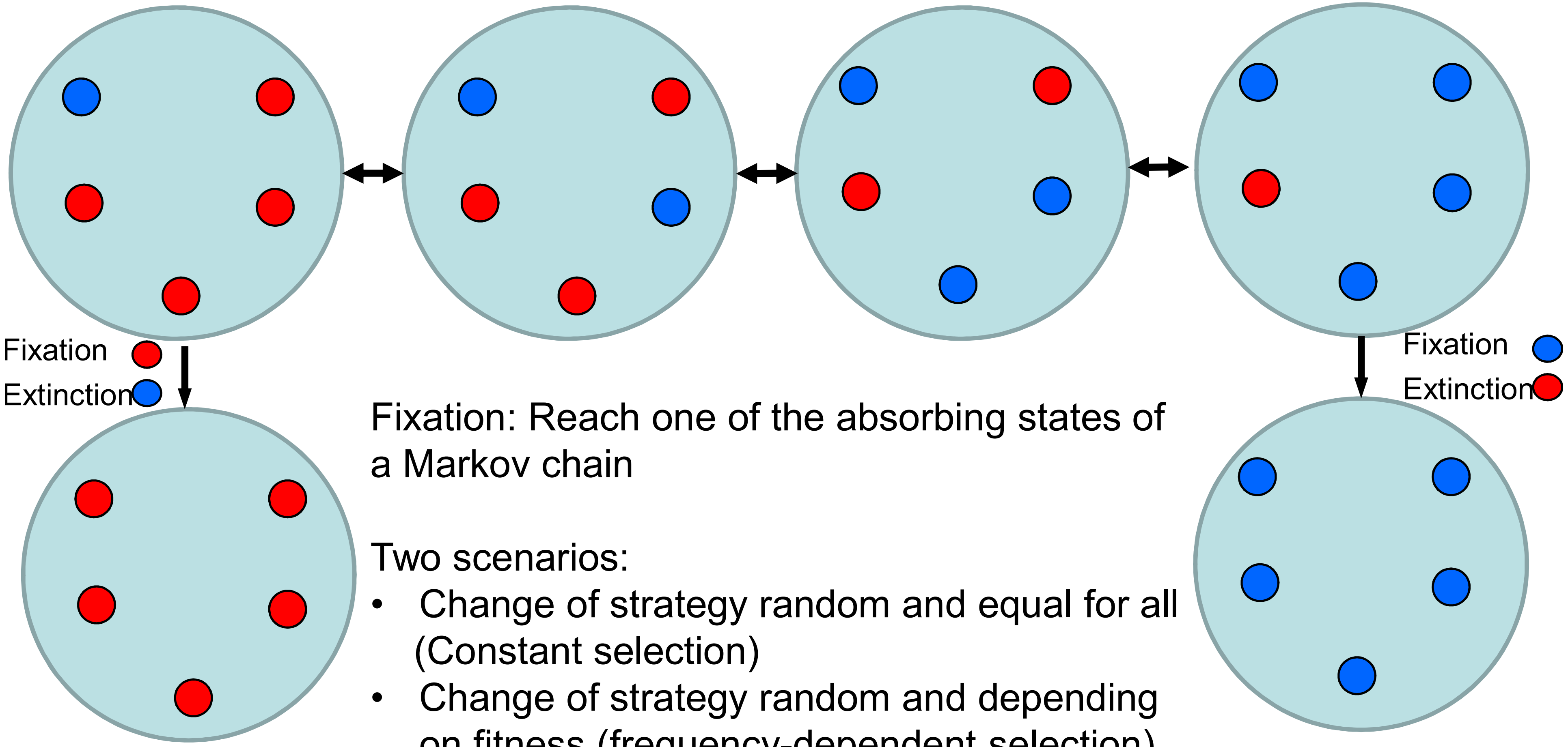


Mutation
= there is
novelty

Selection
= growth is
not equal

Game Dynamics and Fixation Properties: Strategy vector

- **2 strategies, red and blue, one change of strategy once a time**



Fixation: Reach one of the absorbing states of a Markov chain

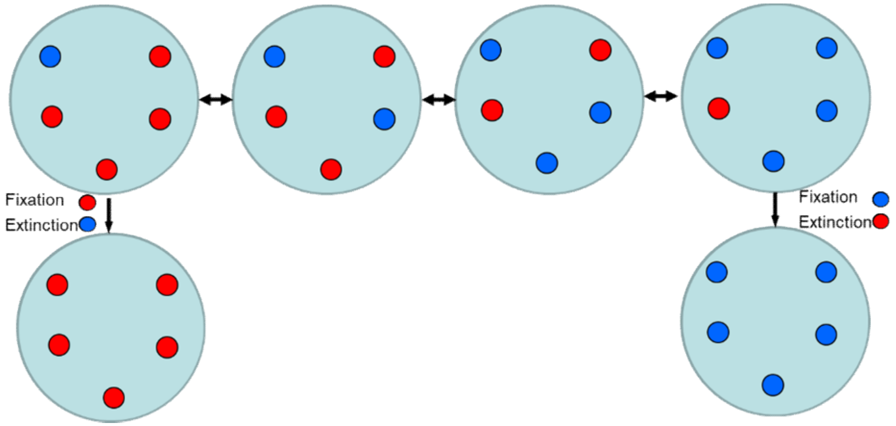
Two scenarios:

- Change of strategy random and equal for all (Constant selection)
- Change of strategy random and depending on fitness (frequency-dependent selection)

Game Dynamics and Fixation Properties: Strategy vector

- **Fixation probabilities**

$$\rho$$



Constant selection: individual payoff (and individual fitness) only depends on own strategy

Neutral evolution: fitness 🔵 = fitness 🔴

$$\rho = \frac{1}{N}$$

Fitness dependent evolution: fitness 🔵 $f \neq 1$

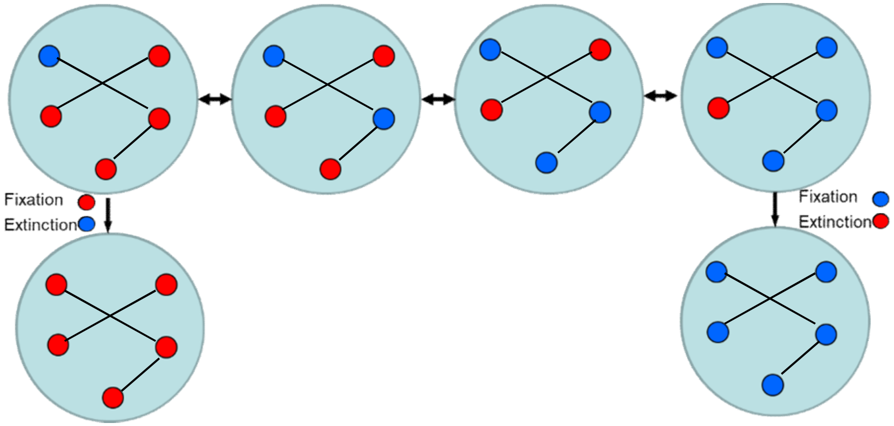
fitness 🔴 $f = 1$

$$\rho_{blue} = \frac{1-1/f}{1-1/f^{N}}$$

Game Dynamics and Fixation Properties: Strategy vector

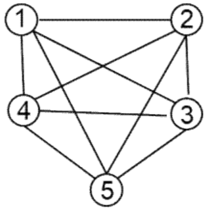
- **Fixation probabilities**

ρ



Frequency-dependent selection (Frequency dependence):
individual payoff (and individual fitness) depends on own strategy

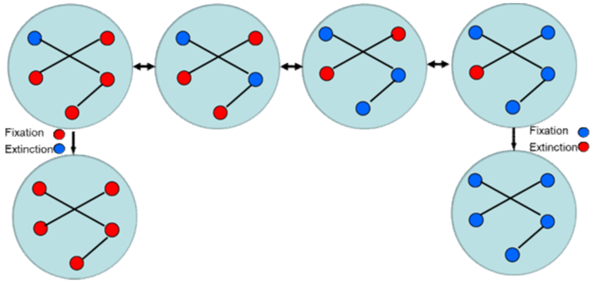
AND
who the coplayers of the individual are → network of interaction



AND
the strategies of the coplayers → strategy vector → configuration

Game Dynamics and Fixation Properties: Strategy vector

Frequency dependence and configurations



- Evolution acts on individuals (more precise on properties of individuals)
- Co-evolutionary games → players with the property strategies

- But: Game dynamics not understandable by the strategy of a player alone
- Need all strategies of all interacting players → frequency-dependence

- Configurations: Alternative to player-centered view
- Enumerates all choices that players have

N players, 2 strategies each

$$\ell = 2^N$$

$$\pi = \left(\pi_1 \pi_2 \pi_3 \ldots \pi_N\right)$$

$$\pi_i \in \{C_i, D_i\} = \{1,0\}$$

Configuration model

Strategies in a population on *N* players:

$$\pi = \left(\pi_1 \pi_2 \pi_3 \ldots \pi_N\right)$$

$$\pi_i \in \left\{C_i, D_i\right\} = \left\{1,0\right\}$$

Game configuration

Describes strategies of all players
(= the game as a whole)

Example

$N = 4$ $\qquad \ell = 2^4 = 16$

$$\pi = \left(\pi_1 \pi_2 \pi_3 \pi_4\right) = (0110)$$

Players 1 & 4 defect
Players 2 & 3 cooperate

Coplayer configuration

Describes strategies of the coplayers
(= the game from the perspective of each player)

For player 1 $\pi_{co} = \left(\pi_2 \pi_3 \pi_4\right) = (110)$

For player 2 $\pi_{co} = \left(\pi_1 \pi_3 \pi_4\right) = (110)$

→ direct calculation of payoffs

Configurations, local frequencies and payoff: Well-mixed

Local frequencies:

$$\pi_{co} = (110) \qquad \varpi^1(110) = 2/3 \qquad \varpi^0(110) = 1/3$$

Player *i* → strategy *1* (cooperating)

$$p_i^1(\pi_{co}) = R\varpi_i^1(\pi_{co}) + S\varpi_i^0(\pi_{co})$$

$$\begin{array}{ccc} & C_j & D_j \\ C_i & R & S \\ D_i & T & P \end{array}$$

Player *i* → strategy *0* (defecting)

$$p_i^0(\pi_{co}) = T\varpi_i^1(\pi_{co}) + P\varpi_i^0(\pi_{co})$$

Payoff depends on the frequency of strategies among coplayers

$$\pi_{co} = (110) \qquad p_i^1(110) = (2R+S)/3 \qquad p_i^0(110) = (2T+P)/3$$

$$\pi_{co} = (100) \qquad p_i^1(100) = (R+2S)/3 \qquad p_i^0(110) = (T+2P)/3$$

Well-mixed population → every player interacts with all other players (*d*=*N*-*1*)

Example: N = 4 players, d = 3 coplayers (well-mixed)

$$\begin{array}{c|cc} & C_j & D_j \\ \hline C_i & 3 & 0 \\ D_i & 5 & 1 \end{array}$$

PD game

$$p_1^1(110) = p_1(1110)$$
$$p_1^0(110) = p_1(0110)$$
$$p_2^1(110) = p_2(1110)$$
$$p_2^0(110) = p_2(1010)$$

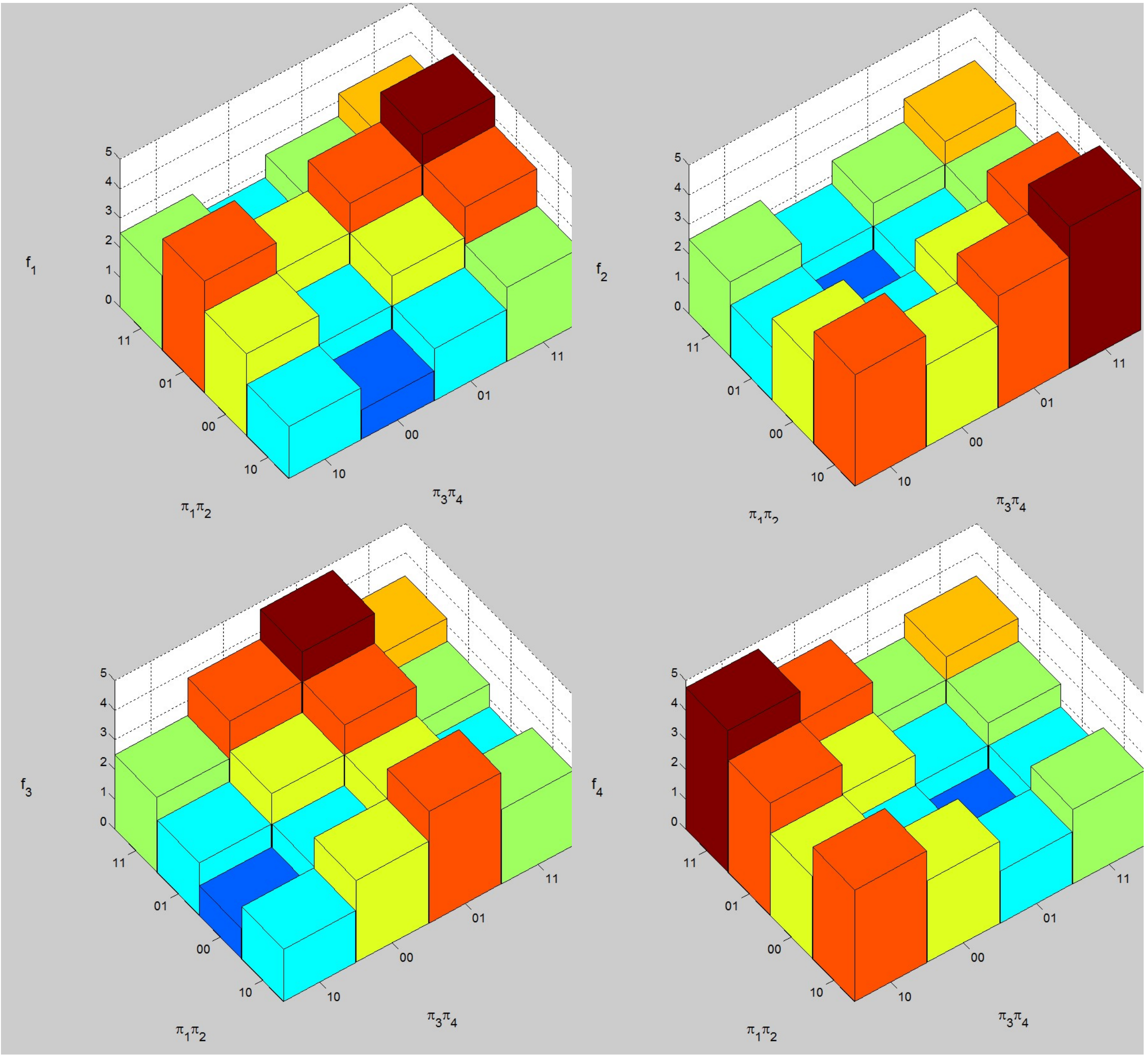
$$A_I = \begin{pmatrix} 0 & 1 & 1 & 1 \\ 1 & 0 & 1 & 1 \\ 1 & 1 & 0 & 1 \\ 1 & 1 & 1 & 0 \end{pmatrix}$$

$$L_3(4) = 1$$

Complete network of interaction

$$f_i = 1 + \delta \cdot \mathrm{p}_i$$

Intensity of selection

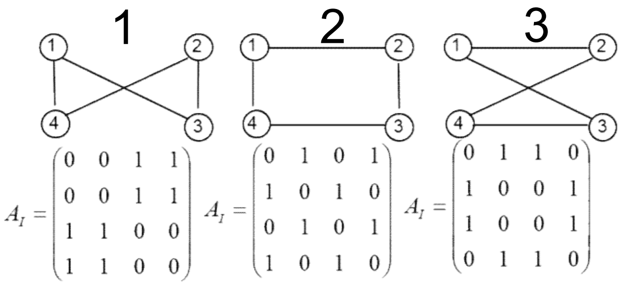


Configurations, local frequencies and payoff: Structured

Structured population: Interaction network structures who-plays-whom

$N = 4, d = 2$

Local frequencies depend on adjacency matrix



$$A_I = \begin{pmatrix} 0 & 0 & 1 & 1 \\ 0 & 0 & 1 & 1 \\ 1 & 1 & 0 & 0 \\ 1 & 1 & 0 & 0 \end{pmatrix} \quad A_I = \begin{pmatrix} 0 & 1 & 0 & 1 \\ 1 & 0 & 1 & 0 \\ 0 & 1 & 0 & 1 \\ 1 & 0 & 1 & 0 \end{pmatrix} \quad A_I = \begin{pmatrix} 0 & 1 & 1 & 0 \\ 1 & 0 & 0 & 1 \\ 1 & 0 & 0 & 1 \\ 0 & 1 & 1 & 0 \end{pmatrix}$$

Configuration (coplayers' strategies for all players)
Interaction network (actually a coplayer ?)

Example: Player 1 + first row of adjacency matrix

$$\pi_{co} = (110) \qquad A_I^{(1)}(1) = (o11) \qquad A_I^{(1)}(2) = (1o1) \qquad A_I^{(1)}(1) = (11o)$$

$$\pi_{co} \circ A_I^{(1)}(1) = (110) \circ (o11) = (o10) \qquad \varpi_1^1(110) = 1/2 = \varpi_1^0(110)$$

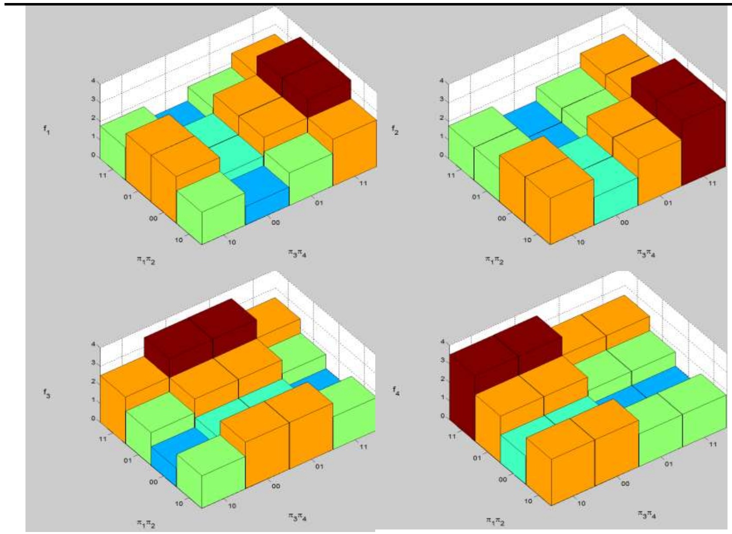
$$\pi_{co} \circ A_I^{(1)}(3) = (110) \circ (11o) = (11o) \qquad \varpi_1^1(110) = 1, \varpi_1^0(110) = 0$$

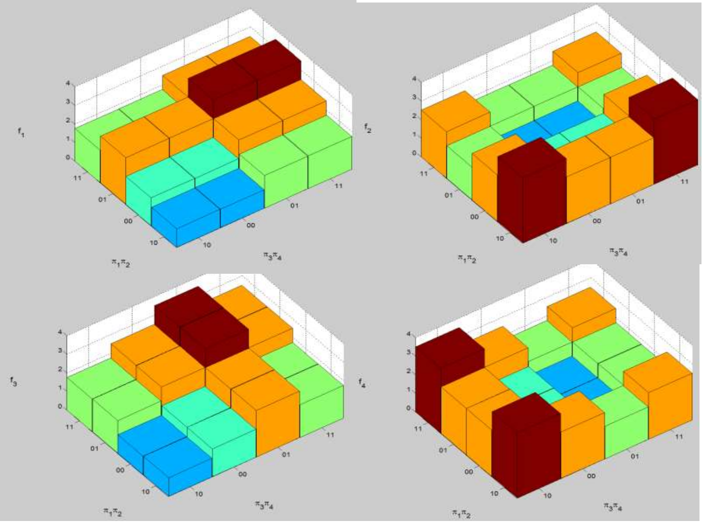
Payoff depends on configuration + interaction network

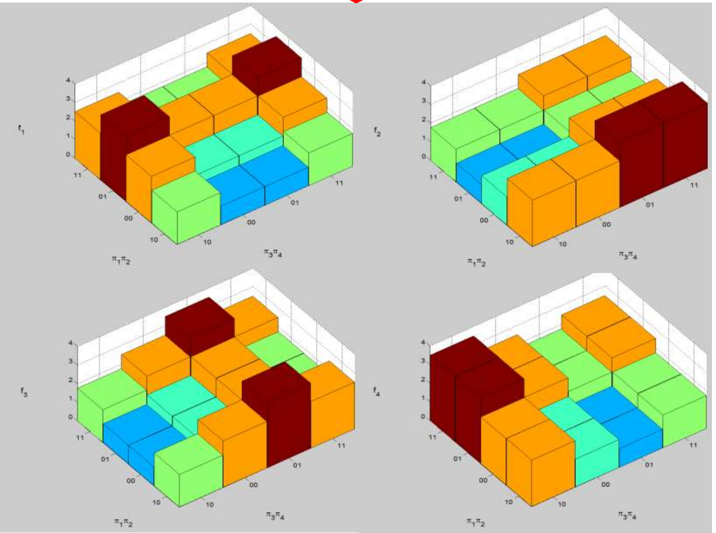
$$p_1^1(110) = (R+S)/2 \qquad p_1^0(110) = (T+P)/2 \qquad A_I(1) \quad A_I(2)$$

$$p_1^1(110) = R \qquad p_1^0(110) = T \qquad A_I(3)$$

Example: N = 4 players, d = 2 coplayers (structured)







$$A_I = \begin{pmatrix} 0 & 0 & 1 & 1 \\ 0 & 0 & 1 & 1 \\ 1 & 1 & 0 & 0 \\ 1 & 1 & 0 & 0 \end{pmatrix} \rightarrow A_I = \begin{pmatrix} 0 & 1 & 0 & 1 \\ 1 & 0 & 1 & 0 \\ 0 & 1 & 0 & 1 \\ 1 & 0 & 1 & 0 \end{pmatrix}$$

$$\downarrow$$

$$A_I = \begin{pmatrix} 0 & 1 & 1 & 0 \\ 1 & 0 & 0 & 1 \\ 1 & 0 & 0 & 1 \\ 0 & 1 & 1 & 0 \end{pmatrix}$$

$$L_2(4) = 3$$

Properties of configuration model of (co)-evolutionary games

- Local frequencies can be calculated for
    - all configurations
    - all players
    - a given network of interaction (well-mixed → complete graph)
(structured → any connected graph)

- Calculating local frequencies is bit-counting (Hamming weight) → linear time complexity

- Payoff is rescaled local frequencies

$$\begin{aligned} p_i^1(\pi_{co}) &= R\varpi_i^1(\pi_{co}) + S\varpi_i^0(\pi_{co}) \\ p_i^0(\pi_{co}) &= T\varpi_i^1(\pi_{co}) + P\varpi_i^0(\pi_{co}) \end{aligned} \qquad \begin{array}{c|cc} & C_j & D_j \\ \hline C_i & R & S \\ D_i & T & P \end{array}$$

- Payoff over varying payoff matrix → linear parametrization

- Shows clearly frequency-dependence (Hamming weight of configuration)

Local frequencies: Configuration + interaction network

Game Dynamics and Fixation Properties: Strategy vector

- **Game playing and updating strategies**

Population of players $$I = (I_1, I_2, \ldots, I_N)$$

Players choose a strategy $$\pi_i(k) = \{C_i, D_i\} = \{1,0\}$$

Collect payoff $$\begin{array}{ccc} & C_j & D_j \\ C_i & R & S \\ D_i & T & P \end{array}$$

Update strategy depending on payoff (replicator rules) $$\pi_i(k+1) = \{C_i \to D_i, D_i \to C_i\} = \{1 \to 0, 0 \to 1\}$$

Q: Given a payoff matrix, replicator rule and an initial configuration of strategies, what is the probability that all players end up with the same strategy?

For instance: $$\pi(0) = (1000\ldots0) \qquad \pi(\infty) = (1111\ldots1)$$
fixation probability of cooperation

Game Dynamics and Fixation Properties: Strategy vector

Replicator dynamics and replicator rules

Players may discard current strategy and adopt neighbor’s strategy

$$\pi_i(k+1) = \{C_i \rightarrow D_i, D_i \rightarrow C_i\} = \{1 \rightarrow 0, 0 \rightarrow 1\}$$

Decision should depend on fitness → success (or failure) of current strategy

Common schemes

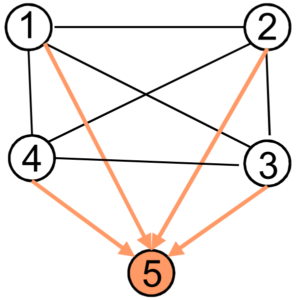
- Death-Birth (DB)
- Birth-Death (BD)
- Pairwise comparison (PC)
- Imitation (IM)

Death-birth (DB) and birth-death (BD) strategy updating

Death-birth (DB)

Choose a player’s strategy to be replaced at random with probability proportional to inverse of fitness (death)

Choose the strategy that replaces at random amongst the remaining players (birth)

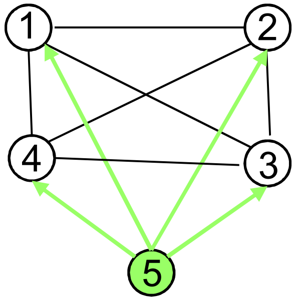


🟠 low fitness

Birth-death (BD)

Choose a player’s strategy to replaced another at random with probability proportional to fitness (birth)

Choose the strategy that is replaced at random amongst the remaining players (death)



🟢 high fitness

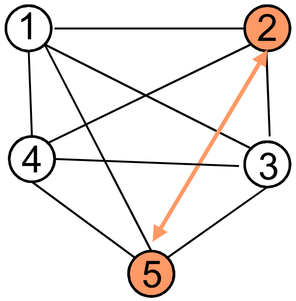
Assumption: Replacement network = interaction network
If not: Breaking symmetry between interaction and replacement (Ohtsuki et al., 2007)

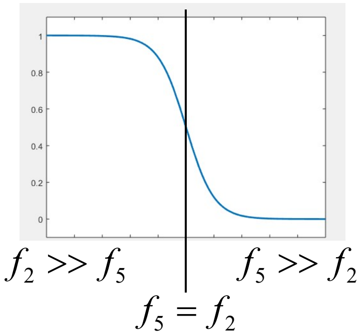
Pairwise comparison (PC) and imitation (IM) strategy updating

Pairwise comparison (PC)

Choose a player’s strategy potentially to be replaced uniformly at random
Choose a potential replacer among the neighbors uniformly at random.

Replace (or preserve) strategy with probability $p(\pi_2 \rightarrow \pi_5) = \frac{1}{1+\exp(f_5 - f_2)}$



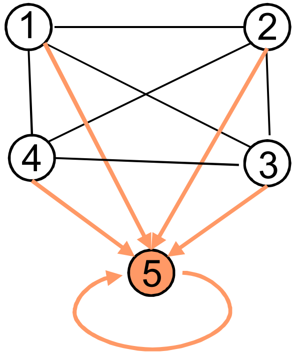


● compare fitness

Imitation (IM)

Choose a player’s strategy to replaced uniformly at random

Choose the strategy that replaces amongst the neighboring players and the player itself proportional to fitness



● high fitness

Game Dynamics and Fixation Properties: Strategy vector

- **Fixation probabilities and fixation times for single cooperators (defectors)**

Fixation probability of cooperation ρ_C

$$\pi(0) = (1000...0) \longrightarrow \pi(\infty) = (1111...1)$$

Fixation probability of defection ρ_D

$$\pi(0) = (0111..1) \longrightarrow \pi(\infty) = (0000...0)$$

absorbing configurations

Generally: both depend on payoff matrix and are not equal but vary over replicator rules and interaction networks

Fixation probability depending on initial player?

$$\left.\begin{matrix} \pi(0) = (1000...0) \\ \pi(0) = (0100...0) \end{matrix}\right. \longrightarrow \pi(\infty) = (1111...1)$$

Well-mixed population (complete interaction network) → no

Structured populations → Not for a single cooperator (and defector) but any other configuration

Game Dynamics and Fixation Properties: Strategy vector

- **Fixation probabilities and fixation times**

average time for

Fixation time of cooperation:

$$\tau_C$$

$$\pi(0) = (1000...0) \longrightarrow \pi(\tau_C) = (1111...1)$$

Fixation time of defection:

$$\tau_D$$

$$\pi(0) = (0111..1) \longrightarrow \pi(\tau_D) = (0000...0)$$

Computational issues: vary (or average) over different start configurations

2^N configurations over $\{0,1\}^N$ $\qquad \dfrac{N}{2^N} \to 0$

Start configurations get rare → final configurations (absorbing configurations) same

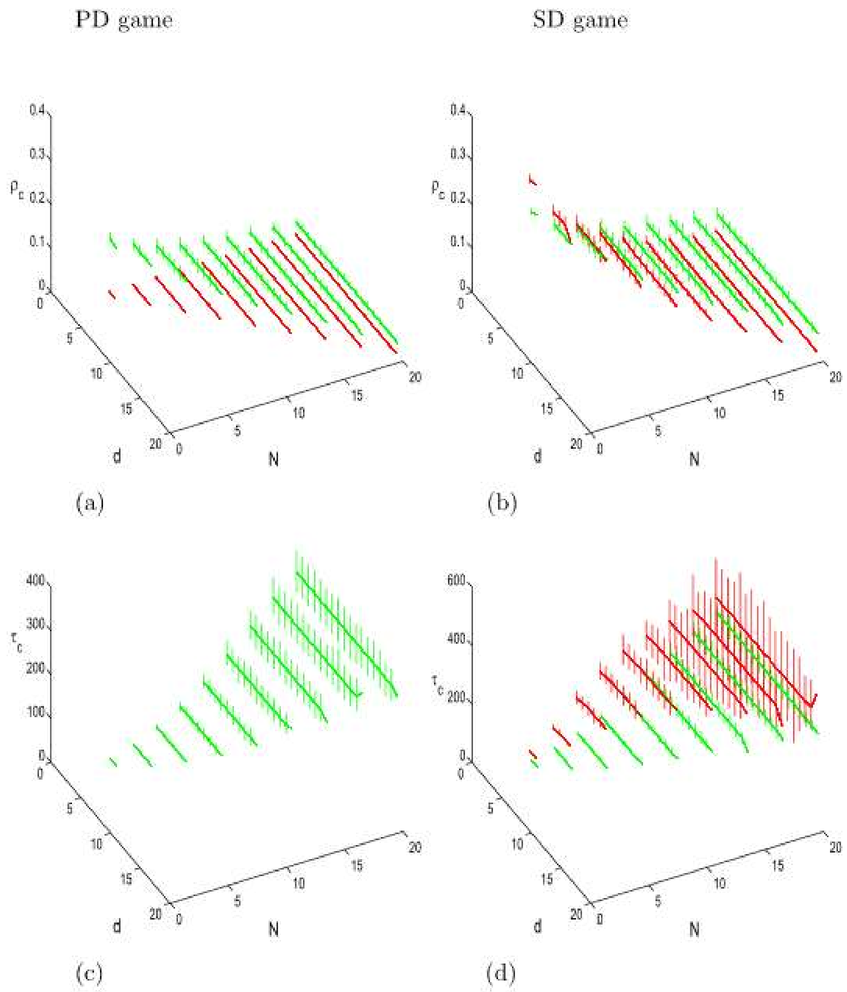
Fixation properties: Example

Fixation properties (probabilities and times) over *N* and *d*

Conclusions about coevolutionary game dynamics:

Properties vary over interaction networks

No fixation for PD BD



red	BD
green	DB

Game Dynamics and Fixation Properties: Strategy vector

- **Fixation probabilities and fixation times: Bad news!**

Calculating fixation probabilities and fixation times in structured populations

→ Computational intractable in general settings
→ Computational cost increases exponential with players and coplayers

BUT: If a game setting favors fixation of a strategy can be answered for

- Random change of strategy equal for all
- Random change of strategy depending on fitness for single cooperator (and single defector)
- Weak selection and any configuration

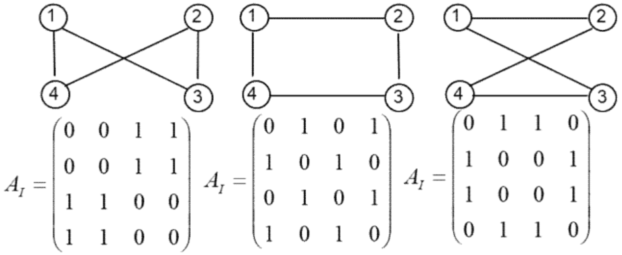
Game Dynamics and Fixation Properties: Strategy vector

- **Game setting favors fixation of a strategy**

Setting: Payoff matrix

$$\begin{array}{ccc} & C_j & D_j \\ C_i & R & S \\ D_i & T & P \end{array}$$

Network of interaction



$$A_I = \begin{pmatrix} 0 & 0 & 1 & 1 \\ 0 & 0 & 1 & 1 \\ 1 & 1 & 0 & 0 \\ 1 & 1 & 0 & 0 \end{pmatrix} \quad A_I = \begin{pmatrix} 0 & 1 & 0 & 1 \\ 1 & 0 & 1 & 0 \\ 0 & 1 & 0 & 1 \\ 1 & 0 & 1 & 0 \end{pmatrix} \quad A_I = \begin{pmatrix} 0 & 1 & 1 & 0 \\ 1 & 0 & 0 & 1 \\ 1 & 0 & 0 & 1 \\ 0 & 1 & 1 & 0 \end{pmatrix}$$

Configuration

$$\pi = \left(\pi_1 \pi_2 \pi_3 \ldots \pi_N\right)$$

d-regular graph on *N* vertices (*N* players, *d* coplayers each)

Strategy C_i is favored over D_i → $\rho_C > \rho_D$

$$\sigma > \frac{T-S}{R-P}$$

Structure coefficient $\sigma = \sigma(N, d, \pi, A_I)$

Q: When does the structure coefficient not depend on configuration and network?

Game Dynamics and Fixation Properties: Strategy vector

- **Generic structure coefficient, *d*-regular graph on *N* vertices**

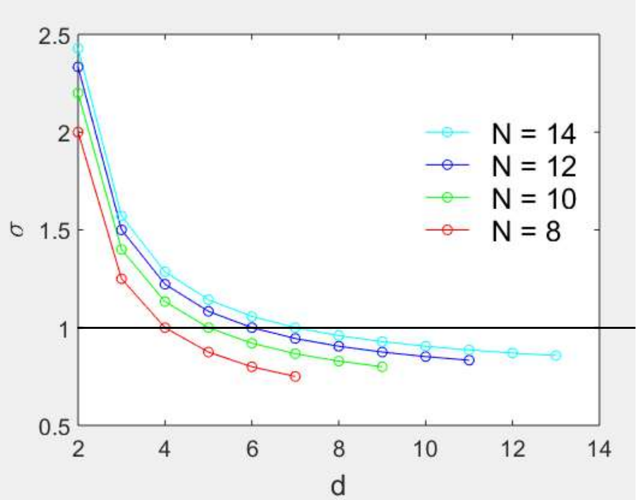
For a single cooperator (and a single defector), (Tarnita et al., 2009)

Well-mixed (*d=N-1*) $\sigma = \frac{N-2}{N}$

Cycle (*d=2*) $\sigma = \frac{3N-8}{N}$

Structured (*N>>d)*
(and DB updating) $\sigma = \frac{d+1}{d-1}$

Any *N* and *d* $\sigma = \frac{(d+1)N-4d}{(d-1)N}$



$$d = \frac{N}{2}$$

Game Dynamics and Fixation Properties: Strategy vector

- **Generic structure coefficient: example**

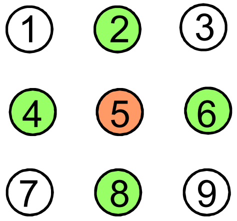
  Evolutionary games on a lattice: DB updating, a single cooperator at initial configuration

  Q: Is fixation of cooperation favored?

$$\begin{array}{ccc} & C_j & D_j \\ C_i & R & S \\ D_i & T & P \end{array}$$

i player   j coplayer

Von Neumann neighborhood



$$A_I = \begin{pmatrix} 0 & 1 & 1 & 1 & 0 & 0 & 1 & 0 & 0 \\ 1 & 0 & 1 & 0 & 1 & 0 & 0 & 1 & 0 \\ 1 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 & 1 & 1 & 1 & 0 & 0 \\ 0 & 1 & 0 & 1 & 0 & 1 & 0 & 1 & 0 \\ 0 & 0 & 1 & 1 & 1 & 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 1 & 0 & 0 & 0 & 1 & 1 \\ 0 & 1 & 0 & 0 & 1 & 0 & 1 & 0 & 1 \\ 0 & 0 & 1 & 0 & 0 & 1 & 1 & 1 & 0 \end{pmatrix}$$

4-regular graph over 9 vertices

$$\sigma = \frac{(d+1)N-4d}{(d-1)N} = \frac{29}{27} > \frac{T-S}{R-P}$$

→ Rescaled payoff matrix $\begin{array}{ccc} & C_j & D_j \\ C_i & R & P-(R-P)v \\ D_i & R+(R-P)u & P \end{array}$

Game Dynamics and Fixation Properties: Strategy vector

- **Generic structure coefficient: example lattice *N=9, d=4***

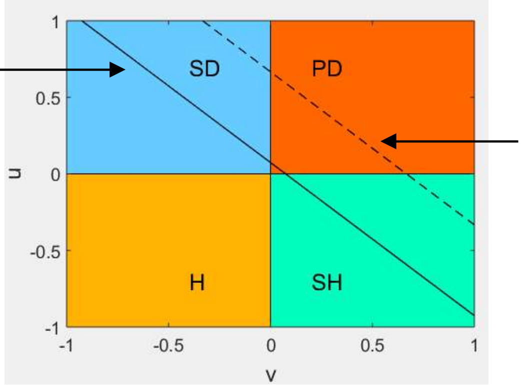
  Evolutionary games on a lattice: DB updating, a single cooperator at initial configuration

  Q: Is fixation of cooperation favored?

→ Rescaled payoff matrix $\begin{array}{cc} & \begin{array}{cc} C_j & D_j \end{array} \\ \begin{array}{c} C_i \\ D_i \end{array} & \begin{pmatrix} R & P-(R-P)v \\ R+(R-P)u & P \end{pmatrix} \end{array}$

$$\sigma = \frac{(d+1)N-4d}{(d-1)N} = \frac{29}{27} > 1+u+v$$

$$u < \frac{2}{27} - v \longrightarrow$$



$$N \to \infty \qquad \sigma = \frac{(d+1)N-4d}{(d-1)N} \to \frac{5}{3}$$

$$\longleftarrow u < \frac{1}{3} - v$$

Structure coefficients: Any configuration

Structure coefficients can be defined for any configurations and any interaction network described by regular graphs (Chen et al., 2016)

Structure coefficients vary over configurations with more than one cooperator (or more than one defector)

Structure coefficients vary over interaction networks

Question of favored strategy more complicated to answer

Initial placement of cooperator to induce fixation properties becomes a design problem

How to define landscapes for coevolutionary games?

- **Fitness landscape view**

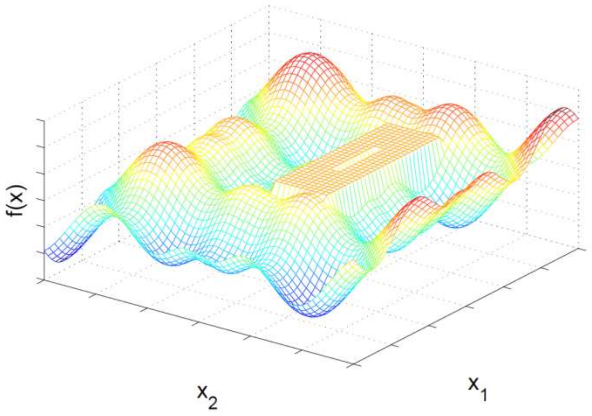
Relationship between genotype, phenotype and fitness
(i.e. all solutions, candidate solutions, solution quality)

Geometric interpretation:
2D fitness landscape metaphor
(valleys, peaks, ridges, plateaus
but also: lakes and flows)

Beyond the metaphor: **Computational Tool**

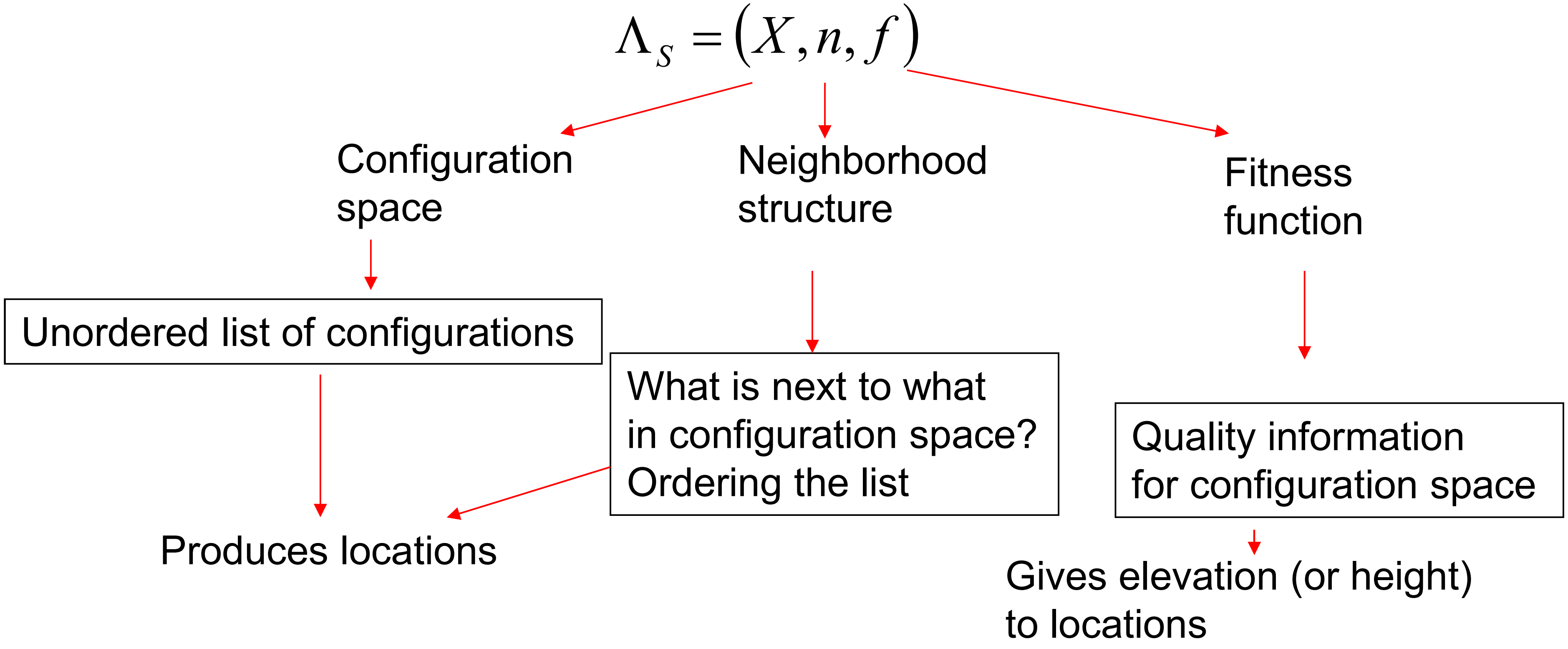
Potentials for (evolutionary) dynamics

(i.e. driving forces behind evolutionary processes)



How to define landscapes for coevolutionary games?

- **Mathematical description of fitness landscape**



$$\Lambda_S = \left(X, n, f\right)$$

Configuration space

Neighborhood structure

Fitness function

Unordered list of configurations

What is next to what in configuration space? Ordering the list

Quality information for configuration space

Produces locations

Gives elevation (or height) to locations

How to define landscapes for coevolutionary games?

Configuration space for coevolutionary games:

At least two possibilities: Players and strategies

Players

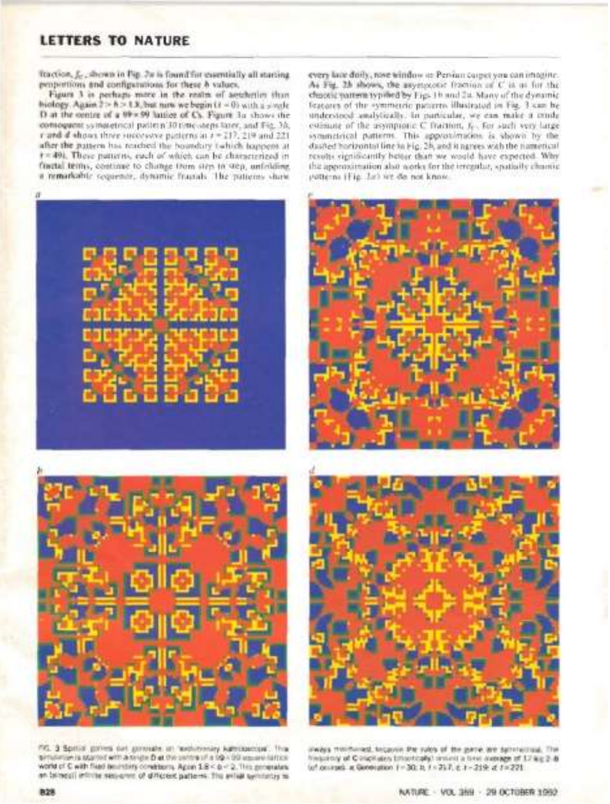
Configuration: all players

Neighbors: players and coplayers

Fitness: payoff (or derived quantities)

But: Payoff frequency-dependent

Changing network of interaction
→ Changing neighborhood structure
Coevolutionary games:
→ Dynamic fitness + changing neighborhood = hard



LETTERS TO NATURE

fraction, f_C, shown in Fig. 2a is found for essentially all starting proportions and configurations for these b values.

Figure 3 is perhaps more in the realm of aesthetics than biology. Again $2 > b > 1.8$, but now we begin ($t = 0$) with a single D at the centre of a 99×99 lattice of Cs. Figure 3a shows the consequent symmetrical pattern 30 time-steps later, and Fig. 3b, c and d shows three successive patterns at $t = 217$, 219 and 221 after the pattern has reached the boundary (which happens at $t = 49$). These patterns, each of which can be characterized in fractal terms, continue to change from step to step, unfolding a remarkable sequence, dynamic fractals. The patterns show every lace doily, rose window or Persian carpet you can imagine. As Fig. 2b shows, the asymptotic fraction of C is as for the chaotic pattern typified by Figs 1b and 2a. Many of the dynamic features of the symmetric patterns illustrated in Fig. 3 can be understood analytically. In particular, we can make a crude estimate of the asymptotic C fraction, f_C, for such very large symmetrical patterns. This approximation is shown by the dashed horizontal line in Fig. 2b, and it agrees with the numerical results significantly better than we would have expected. Why the approximation also works for the irregular, spatially chaotic patterns (Fig. 2a) we do not know.

FIG. 3 Spatial games can generate an 'evolutionary kaleidoscope'. This simulation is started with a single D at the centre of a 99×99 square lattice world of C with fixed boundary conditions. Again $1.8 < b < 2$. This generates an (almost) infinite sequence of different patterns. The initial symmetry is always maintained, because the rules of the game are symmetrical. The frequency of C oscillates (chaotically) around a time average of 12 log 2-8 (of course). a, Generation $t = 30$; b, $t = 217$; c, $t = 219$; d, $t = 221$.

828 NATURE · VOL 359 · 29 OCTOBER 1992

Nowak & May, 1992

How to define landscapes for coevolutionary games?

Configuration space for coevolutionary games:

At least two possibilities

Strategies

Configuration: strategy distribution of all players $X = \Pi, \ell = 2^N$

Neighbors: strategy distribution after one strategy updating (Hamming distance 1)

Fitness: payoff (or derived quantities), static and unique for a given network

Example: $N = 4$ players, two strategies (C=1,D=0) → $\ell = 2^4 = 16$ elements

$\pi = (\pi_1 \pi_2 \pi_3 \pi_4) = (0101)$ player 2&4 cooperate, 1&3 defect

player 1 changes strategy

$\pi = (\pi_1 \pi_2 \pi_3 \pi_4) = (1101)$

Dynamic landscapes for coevolutionary games

From strategy landscapes to game landscapes

Strategy landscapes are building blocks for game landscapes
for a given strategy updating process

→ Take death and birth probabilities according to the transition probabilities for BD and DB updating (Pattni et al, 2015)

→ Decompose strategy landscape and summarize probabilities over the strategy landscape

→ Obtain game landscape for BD and DB updating process (strategy updating breaks symmetry of the strategy landscapes) (Richter, 2017)

Summary and research questions

- **Coevolutionary games complete by three entities**
  - **Payoff matrix**
  - **Strategy vector → configuration**
  - **Interaction network**

- **Payoff matrix** → universal scaling, Wang et al. (2015), convenient way to study relevant game-theoretical settings in a 2D parameter space

- **Strategy vector → configuration,** Chen et al. (2016), describes evolutionary game complete (all possible combinations of strategies)

BUT: computational issues $\ell = 2^N$(in principle, intractable for larger *N*)

How many of the N players are cooperators (or defectors)?

Configurations → Hamming weight of π $\pi = \left(\pi_1\pi_2\pi_3\pi_4\right) = \left(0101\right)$ $c(\pi) = hw(\pi) = 2$

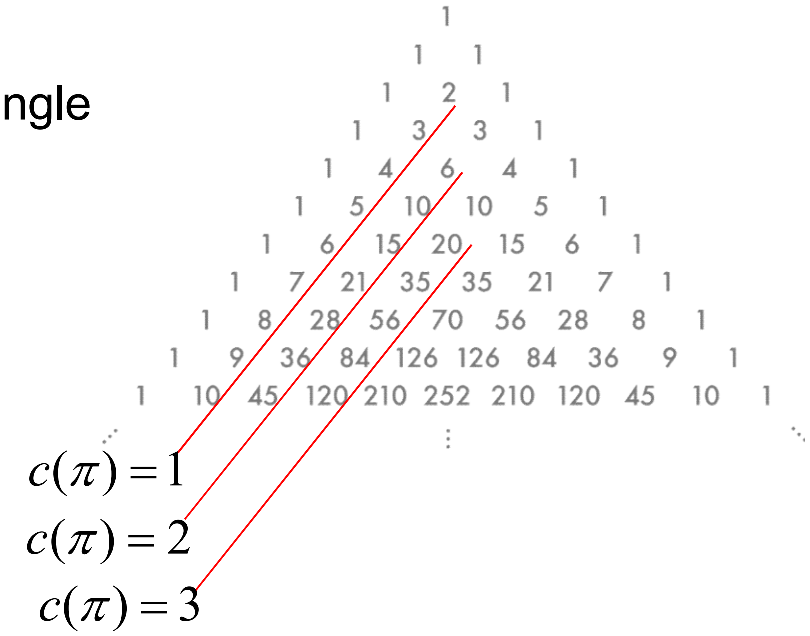
How many of the $\ell = 2^4 = 16$ have $c(\pi) = hw(\pi) = 2$ → $\begin{pmatrix} N \\ c(\pi) \end{pmatrix} = \begin{pmatrix} 4 \\ 2 \end{pmatrix} = 6$
(2 cooperators)?

Summary and research questions

- **Strategy vector → configuration**

How many of the $\ell = 2^4 = 16$ have (2 cooperators)? $c(\pi) = hw(\pi) = 2$ → $\binom{N}{c(\pi)} = \binom{4}{2} = 6$

General: Binomial coefficients $\binom{N}{c(\pi)}$ Pascal triangle



$c(\pi) = 1$

$c(\pi) = 2$

$c(\pi) = 3$

1 cooperator → linear
2 cooperators → quadratic
3 cooperators → cubic

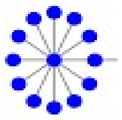
$\frac{N}{2}$ cooperators (*N* large) → exponential

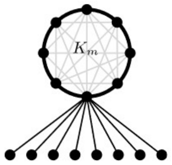
Computational complexity not for all configurations
Initial placement of cooperators → not generally intractable
Design: Optimal initial configuration → fixation → promotion of cooperation

Summary and research questions

Interaction network

Substantial amount of results for regular graphs (including complete graphs → well-mixed case, and cycles)





also for special graphs structures (stars, comets)

based on structure coefficients

But: How many different interaction networks there are?
Not answerable exactly even for *d*-regular graphs on *N* vertices

Asymptotic approximation: $d = o\left(\sqrt{N}\right)$ $L_d = O\left(N^N\right), d << N$

Grows faster than configurations

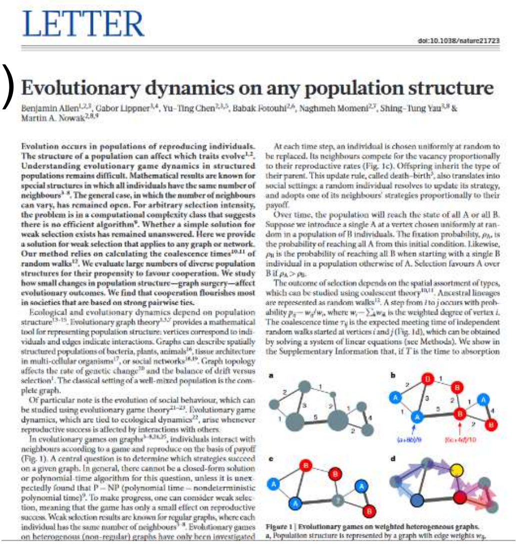
Design: Optimal interaction network → fixation → promotion of cooperation

Summary and research questions

- **Interaction network**

Research question: Extend to general graph structure

Recent work, Allen et al. (2017), calculate fixation
properties for any network
Coalescences times (meeting times of random walks on the interaction graph)
→ Structure coefficient for any graph and a single cooperator
→ Calculation in polynomial time
→ Open questions:
  → extend to any configuration (more than one cooperator)
  → extend to beyond weak selection, $f_i = 1 + \delta p_i$



LETTER

doi:10.1038/nature21723

Evolutionary dynamics on any population structure

Benjamin Allen[1,2,3], Gabor Lippner[3,4], Yu-Ting Chen[2,3,5], Babak Fotouhi[2,6], Naghmeh Momeni[2,7], Shing-Tung Yau[3,8] & Martin A. Nowak[2,8,9]

Evolution occurs in populations of reproducing individuals. The structure of a population can affect which traits evolve[1,2]. Understanding evolutionary game dynamics in structured populations remains difficult. Mathematical results are known for special structures in which all individuals have the same number of neighbours[3-8]. The general case, in which the number of neighbours can vary, has remained open. For arbitrary selection intensity, the problem is in a computational complexity class that suggests there is no efficient algorithm[9]. Whether a simple solution for weak selection exists has remained unanswered. Here we provide a solution for weak selection that applies to any graph or network. Our method relies on calculating the coalescence times[10,11] of random walks[12]. We evaluate large numbers of diverse population structures for their propensity to favour cooperation. We study how small changes in population structure—graph surgery—affect evolutionary outcomes. We find that cooperation flourishes most in societies that are based on strong pairwise ties.

Ecological and evolutionary dynamics depend on population structure[13-15]. Evolutionary graph theory[3,5,7] provides a mathematical tool for representing population structure: vertices correspond to individuals and edges indicate interactions. Graphs can describe spatially structured populations of bacteria, plants, animals[16], tissue architecture in multi-cellular organisms[17], or social networks[18,19]. Graph topology affects the rate of genetic change[20] and the balance of drift versus selection[1]. The classical setting of a well-mixed population is the complete graph.

Of particular note is the evolution of social behaviour, which can be studied using evolutionary game theory[21-23]. Evolutionary game dynamics, which are tied to ecological dynamics[22], arise whenever reproductive success is affected by interactions with others.

In evolutionary games on graphs[3-8,24,25], individuals interact with neighbours according to a game and reproduce on the basis of payoff (Fig. 1). A central question is to determine which strategies succeed on a given graph. In general, there cannot be a closed-form solution or polynomial-time algorithm for this question, unless it is unexpectedly found that P = NP (polynomial time = nondeterministic polynomial time)[9]. To make progress, one can consider weak selection, meaning that the game has only a small effect on reproductive success. Weak selection results are known for regular graphs, where each individual has the same number of neighbours[3-8]. Evolutionary games on heterogenous (non-regular) graphs have only been investigated

At each time step, an individual is chosen uniformly at random to be replaced. Its neighbours compete for the vacancy proportionally to their reproductive rates (Fig. 1c). Offspring inherit the type of their parent. This update rule, called death–birth[3], also translates into social settings: a random individual resolves to update its strategy, and adopts one of its neighbours' strategies proportionally to their payoff.

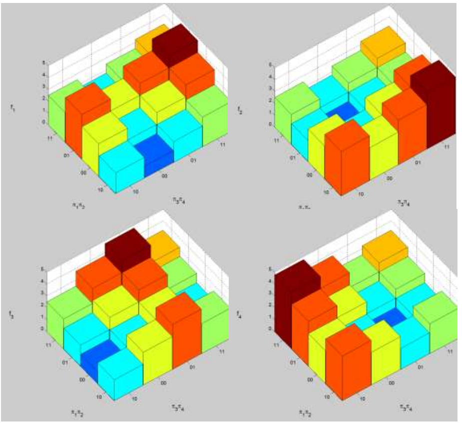
Over time, the population will reach the state of all A or all B. Suppose we introduce a single A at a vertex chosen uniformly at random in a population of B individuals. The fixation probability, ρ_A, is the probability of reaching all A from this initial condition. Likewise, ρ_B is the probability of reaching all B when starting with a single B individual in a population otherwise of A. Selection favours A over B if $\rho_A > \rho_B$.

The outcome of selection depends on the spatial assortment of types, which can be studied using coalescent theory[10,11]. Ancestral lineages are represented as random walks[12]. A step from i to j occurs with probability $p_{ij} = w_{ij}/w_i$, where $w_i = \sum_k w_{ik}$ is the weighted degree of vertex i. The coalescence time τ_{ij} is the expected meeting time of independent random walks started at vertices i and j (Fig. 1d), which can be obtained by solving a system of linear equations (see Methods). We show in the Supplementary Information that, if T is the time to absorption

Figure 1 | Evolutionary games on weighted heterogeneous graphs. **a**, Population structure is represented by a graph with edge weights w_{ij}.

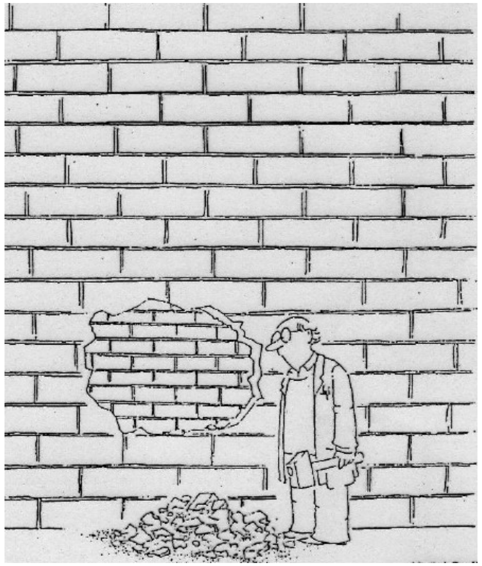
Research directions

- Co-evolutionary game dynamics
- Conditions for obtaining certain fixation properties → how to promote (or suppress) cooperation
- Beyond single cooperators (single defectors)
- Beyond weak selection
- Interplay between strategies (configurations) and interaction network



Thank you !

Questions ?



Hendrik Richter

HTWK Leipzig University of Applied Sciences
Leipzig, Germany

hendrik.richter@htwk-leipzig
http://www.eit.htwk-leipzig.de/~richter

References

- **Allen, B., Nowak, M. A., 2014. Games on graphs. EMS Surv. Math. Sci. 1,113–151.**

- **Allen, B., Lippner, G., Chen, Y. T., Fotouhi, B., Momeni, N., Yau, S. T., Nowak, M. A., 2017. Evolutionary dynamics on any population structure. Nature 544, 227–230.**

- **Bayati, M., Kim, J. H., Saberi, A., 2010. A sequential algorithm for generating random graphs. Algorithmica 58, 860–910.**

- **Chen, Y. T., 2013. Sharp benefit–to–cost rules for the evolution of cooperation on regular graphs. Ann. Appl. Probab. 3, 637–664.**

- **Chen, Y. T., McAvoy, A., Nowak, M. A. 2016. Fixation probabilities for any configuration of two strategies on regular graphs. Sci. Rep. 6, 39181.**

- **Lieberman, E., Hauert, C., Nowak, M. A., 2005. Evolutionary dynamics on graphs. Nature 433, 312–316.**

- **Nowak, M. A., May, R. M., 1993. The spatial dilemmas of evolution. Int. J. Bifurc. Chaos 3, 35–78, 1993.**

- **Pattni, K., Broom, M., Silvers, L., Rychtar, J., 2015. Evolutionary graph theory revisited: When is an evolutionary process equivalent to the Moran process? Proc. Roy. Soc. A471, 20150334**

- **Richter, H., 2017. Dynamic landscape models of coevolutionary games. BioSystems 153–154, 26–44.**

- **Tarnita, C. E., Ohtsuki, H., Antal, T., Fu, F., Nowak, M. A., 2009. Strategy selection in structured populations. J. Theor. Biol. 259, 570–581.**

- **Wang, Z., Kokubo, S., Jusup, M., Tanimoto, J., 2015. Universal scaling for the dilemma strength in evolutionary games. Phys. Life Rev. 14: 1–30.**

- **Wormald, N. C. 1999. Models of random regular graphs. In: Lamb, J. D., Preece, D. A. (Eds.), Surveys in Combinatorics, London Mathematical Society Lecture Note Series, vol. 267, Cambridge University Press, Cambridge, pp. 239–298.**

Updating strategy and network of interaction

Strategy updating:	birth-death updating (BD) death-birth updating (DB)

→ No details here, but transition probabilities for strategies can be calculated (Pattni et al.,2015)

Network of interaction updating:	Assume that number of coplayers for each player the same and constant
Network of interaction	→ d-regular graph
Instances of network of interaction	→ instance of a random d-regular graph

Calculating BD and DB game landscapes

Strategy landscape for i-th player

$$\Lambda_{\Pi}^{i}=\left(\Pi,H_{d}{}^{1},f\right)=\left\{\lambda_{\ell}{}^{i}\right\},\ell=1,2,\ldots,2^{N}$$

Decomposed landscape

BD updating

$$b_{\ell}^{i}=\frac{\lambda_{\ell}^{i}}{\sum_{\ell=1}^{2^N}\lambda_{\ell}^{i}}$$

$$d_{i}=\frac{1}{N}\sum_{j=1}^{n}\frac{w_{ji}}{\sum_{\ell=1}^{N}w_{ji}}$$

Replacement restrictions according to replacement matrix

$$W_R=\left\{w_{ij}\right\}$$

DB updating

$$d_{\ell}^{i}=1-\frac{\lambda_{\ell}^{i}}{\sum_{\ell=1}^{2^N}\lambda_{\ell}^{i}}$$

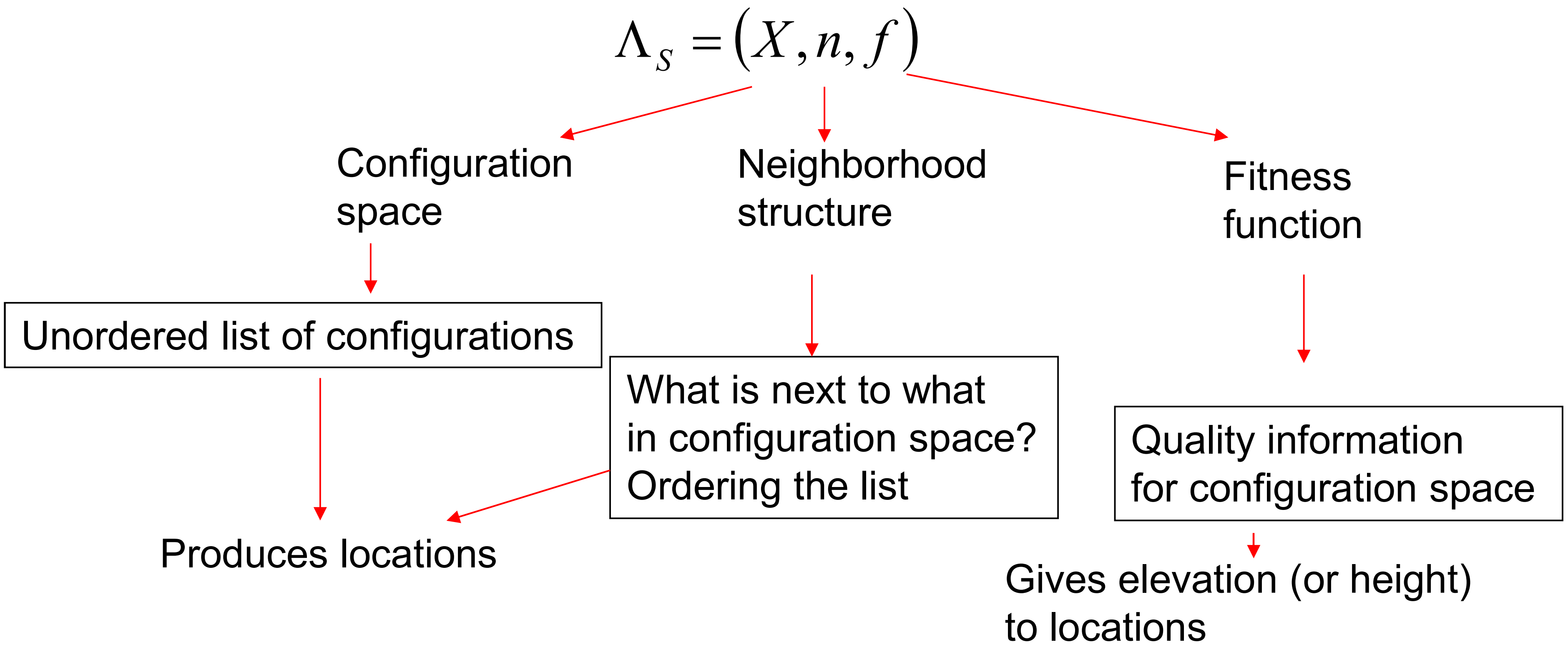
$$b_{i}=\frac{1}{N}\sum_{j=1}^{n}\frac{w_{ij}}{\sum_{\ell=1}^{N}w_{ij}}$$

$$\Lambda_{\Pi}^{BD}=\left\{\lambda_{\ell}{}^{BD}\right\}=\frac{1}{1+\exp\left(\frac{1}{N}\sum_{i=1}^{N}b_{\ell}^{i}d_{i}\right)}$$

$$\Lambda_{\Pi}^{DB}=\left\{\lambda_{\ell}{}^{DB}\right\}=\frac{1}{1+\exp\left(\frac{1}{N}\sum_{i=1}^{N}d_{\ell}^{i}b_{i}\right)}$$

How to define landscapes for coevolutionary games?

- **Mathematical description of fitness landscape**



$$\Lambda_S = \left(X, n, f\right)$$

Configuration space

Neighborhood structure

Fitness function

Unordered list of configurations

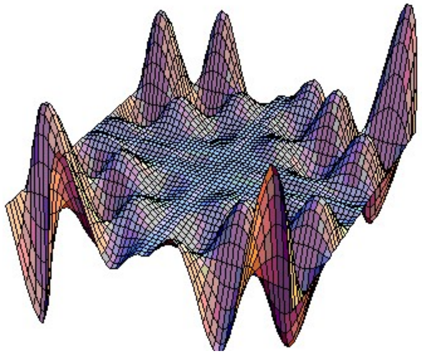
What is next to what in configuration space? Ordering the list

Quality information for configuration space

Produces locations

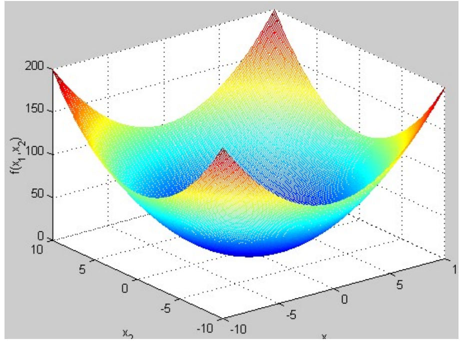
Gives elevation (or height) to locations

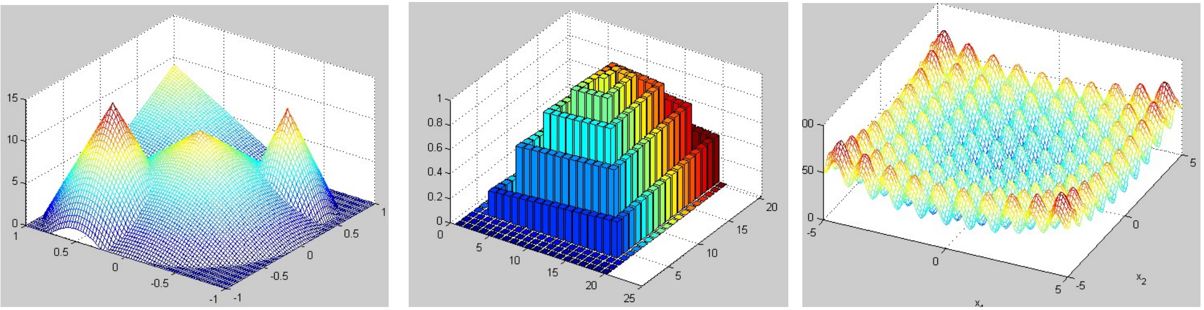
Landscape measures: How likely are evolutionary paths?

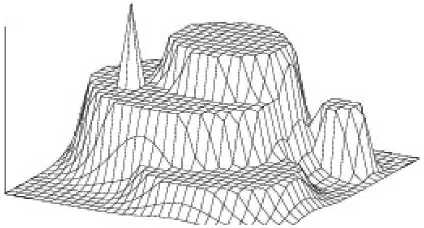


Evaluation of behavior and performance of an evolutionary algorithm
→ Landscape measures (= defining metrics)

No simple answer to how likely evolutionary paths in a certain landscape are.







Easy

More difficult

Landscape measures: Game landscapes

Ruggedness: Correlation structure

How is it calculated?

1. Doing a random walk on the landscape and recording the heights.

$$h(\tau,k) = h(i(\tau), j(\tau), k), \tau = 1,2,...,T.$$

2. Calculating the autocorrelation function with time lag t_L

$$r(t_L,k) = \frac{\sum_{\tau=1}^{T-t_L} (h(\tau,k) - \bar{h}(k)) \cdot (h(\tau + t_L, k) - \bar{h}(k))}{\sum_{\tau=1}^{T} (h(\tau,k) - \bar{h}(k))^2}$$

$$\bar{h}(k) = \sum_{\tau=1}^{T} h(\tau,k)$$

3. Taking the time average of the correlation length $\lambda = -\frac{1}{\ln(r(1))}, r(1) = \langle r(1,k) \rangle$

Landscape measures: Game landscapes

Information content: An entropic measure

How is it calculated?

1. Doing a random walk on the landscape and recording the heights.

$$h(\tau,k)=h(i(\tau),j(\tau),k),\tau=1,2,...,T.$$

2. Coding fitness differences with sensitivity e

$$s_\tau(e,k)=\begin{cases}-1 & if\ h(\tau+1,k)-h(\tau,k)<e\\ 0 & if\ \left|h(\tau+1,k)-h(\tau,k)\right|\le e\\ 1 & if\ h(\tau+1,k)-h(\tau,k)>e\end{cases}$$

$$S(e,k)=s_1s_2...s_{T-1}$$

3. Calculating the probability of the occurrence of the pattern

$$s_\tau s_{\tau+1}\in\{01,0-1,10,1-1,-10,-11\}\rightarrow\{p_{01},p_{0-1},p_{10},p_{1-1}p_{-10},p_{-11}\}$$

4. Obtaining the information content

$$H_{IC}(e,k)=-\sum_{\substack{a,b\in\{-1,0,1\}\\ a\neq b}}p_{ab}(e,k)\log_6 p_{ab}(e,k)$$

$$H_{IC}=H_{IC}(e)\big|_{e=0}=\langle H_{IC}(k)\rangle$$

Landscape measures: Game landscapes

Modality: Number of (local) optima

Ruggedness: Correlation structure

Information content: An entropic measure

Defining a neighborhood structure

Hamming distance

$$\pi = (\pi_1 \pi_2 \pi_3 \pi_4) = (0101) \xrightarrow{N \text{ neighbors}} \pi = (1101, 0001, 0111, 0100)$$

Calculating the number of local optima by enumeration

Landscape measures: Game landscapes

Modality: Number of (local) optima

Ruggedness: Correlation structure

Information content: An entropic measure

Degree of correlation between neighboring points in the landscape

Smooth landscape → similar fitness values → high correlation

Rugged landscape → dramatically different fitness values → low correlation

Standard procedure: Analyzing the correlation structure of a random walk on the landscape

Landscape measures: Game landscapes

Modality: Number of (local) optima
Ruggedness: Correlation structure
Information content: An entropic measure

Amount of information required for describing the landscape

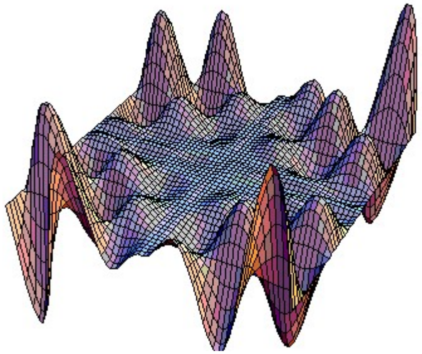
Accounts for diversity and distribution of landscape features as flat areas and optima

Entropic measure of differences in the fitness value of neighboring points

Standard procedure: Analyzing the information structure of a random walk on the landscape

Landscape measures: How likely are evolutionary paths?

Features contributing to problem hardness



→ Number of optima
→ Distribution in search space
→ Nature of the space between them

Another question: How do these features balance each other in terms of problem hardness ?

Landscape measures

→ Modality → Number of (local) optima
→ Ruggedness → Correlation structure
→ Information content → An entropic measure

Compressing complex landscape features in (hopefully meaningful) numbers

Example: N = 4 players, d = 3 coplayers (static landscape)

$$\begin{array}{ccc} & C_j & D_j \\ C_i & 3 & 0 \\ D_i & 5 & 1 \end{array}$$

PD game

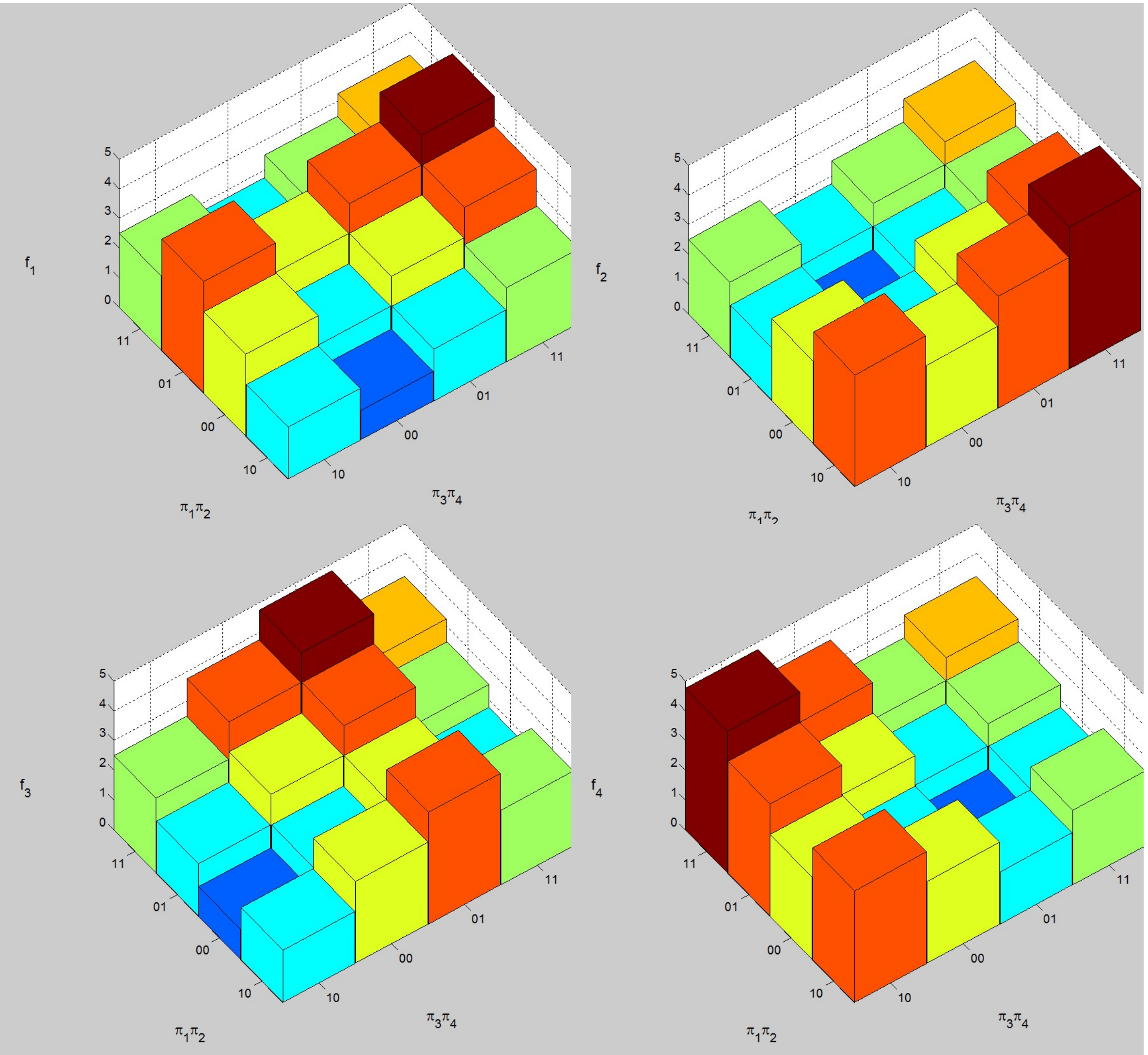
$$A_I = \begin{pmatrix} 0 & 1 & 1 & 1 \\ 1 & 0 & 1 & 1 \\ 1 & 1 & 0 & 1 \\ 1 & 1 & 1 & 0 \end{pmatrix}$$

$$L_3(4) = 1$$

Complete network of interaction

$$fit = 1 + \delta \cdot \text{payoff}$$

Intensity of selection



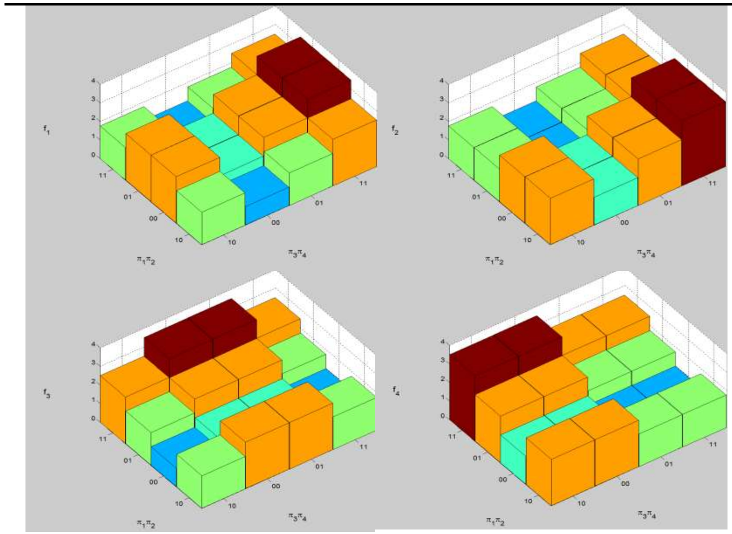
Dynamic landscapes for coevolutionary games

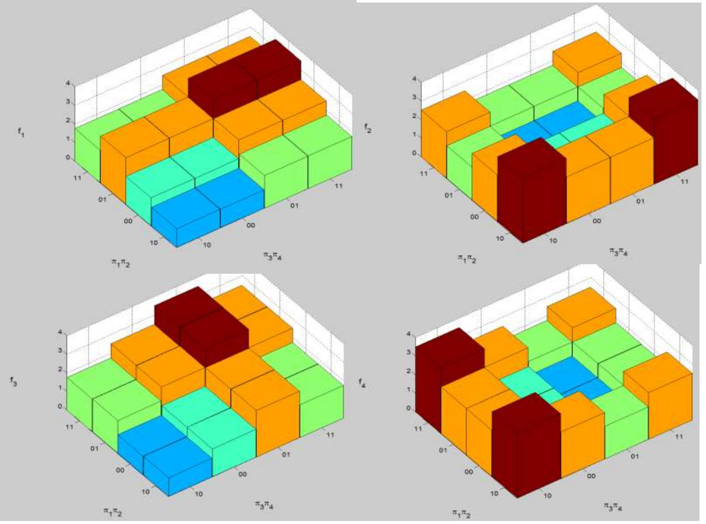
Vary the network of interaction

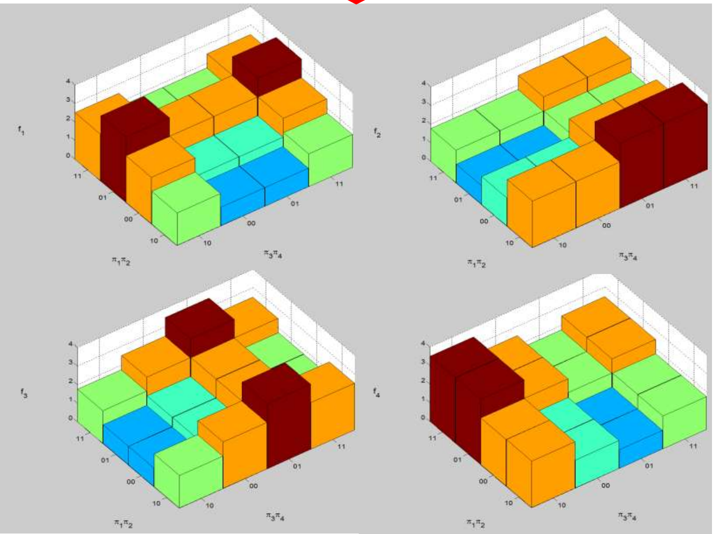
Instance of random d-regular graphs produces instance of the strategy landscape

Instances interpreted as a series of landscapes → dynamic landscape

Example: N = 4 players, d = 2 coplayers (dynamic landscape)







$$A_I = \begin{pmatrix} 0 & 0 & 1 & 1 \\ 0 & 0 & 1 & 1 \\ 1 & 1 & 0 & 0 \\ 1 & 1 & 0 & 0 \end{pmatrix} \longrightarrow A_I = \begin{pmatrix} 0 & 1 & 0 & 1 \\ 1 & 0 & 1 & 0 \\ 0 & 1 & 0 & 1 \\ 1 & 0 & 1 & 0 \end{pmatrix}$$

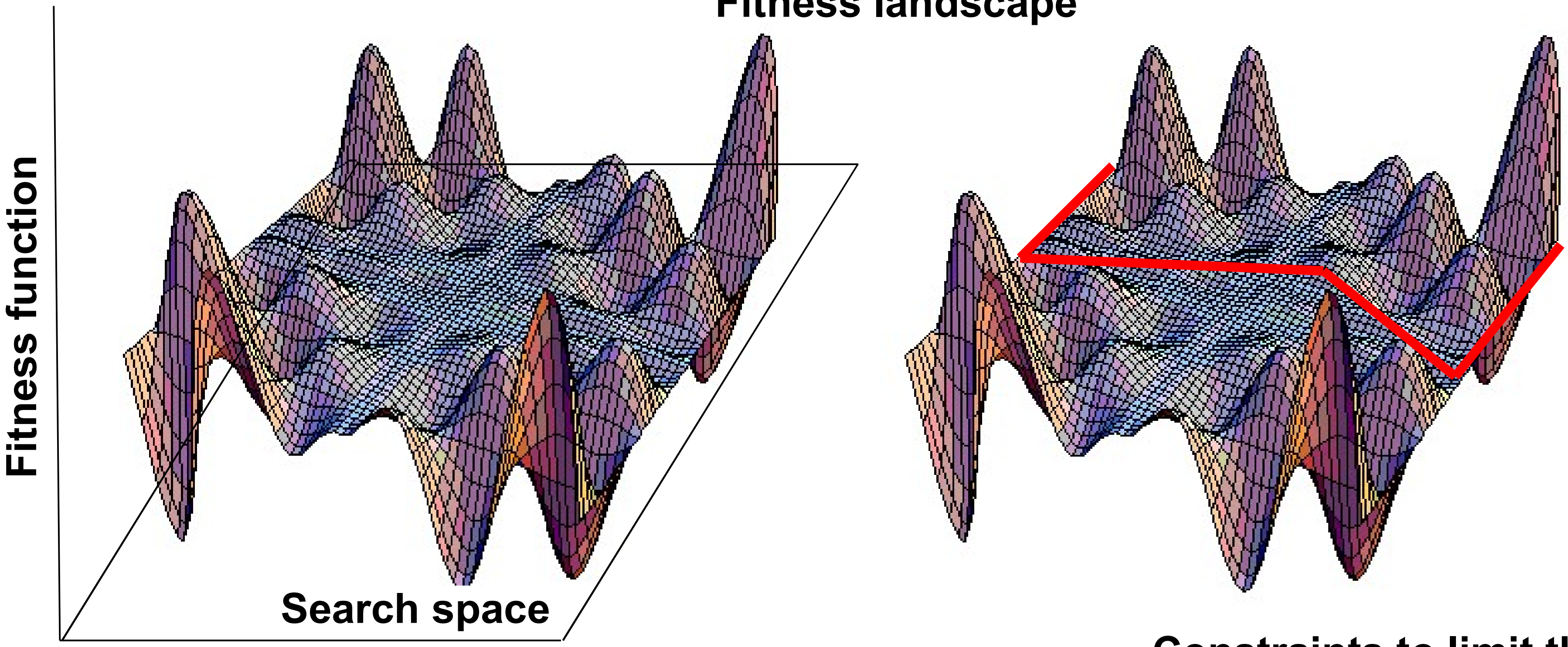
$$\downarrow$$

$$A_I = \begin{pmatrix} 0 & 1 & 1 & 0 \\ 1 & 0 & 0 & 1 \\ 1 & 0 & 0 & 1 \\ 0 & 1 & 1 & 0 \end{pmatrix}$$

$$L_2(4) = 3$$

Structure and geometry of configuration space and fitness function

Fitness landscape



General topology

Constraints to limit the feasible search space

Immediate 'geographic' consequences: mountains and valleys → topology
Further consequences: lakes and flows → evolutionary dynamics
→ evolutionary paths

What is fitness landscape? The ideas of evolutionary paths

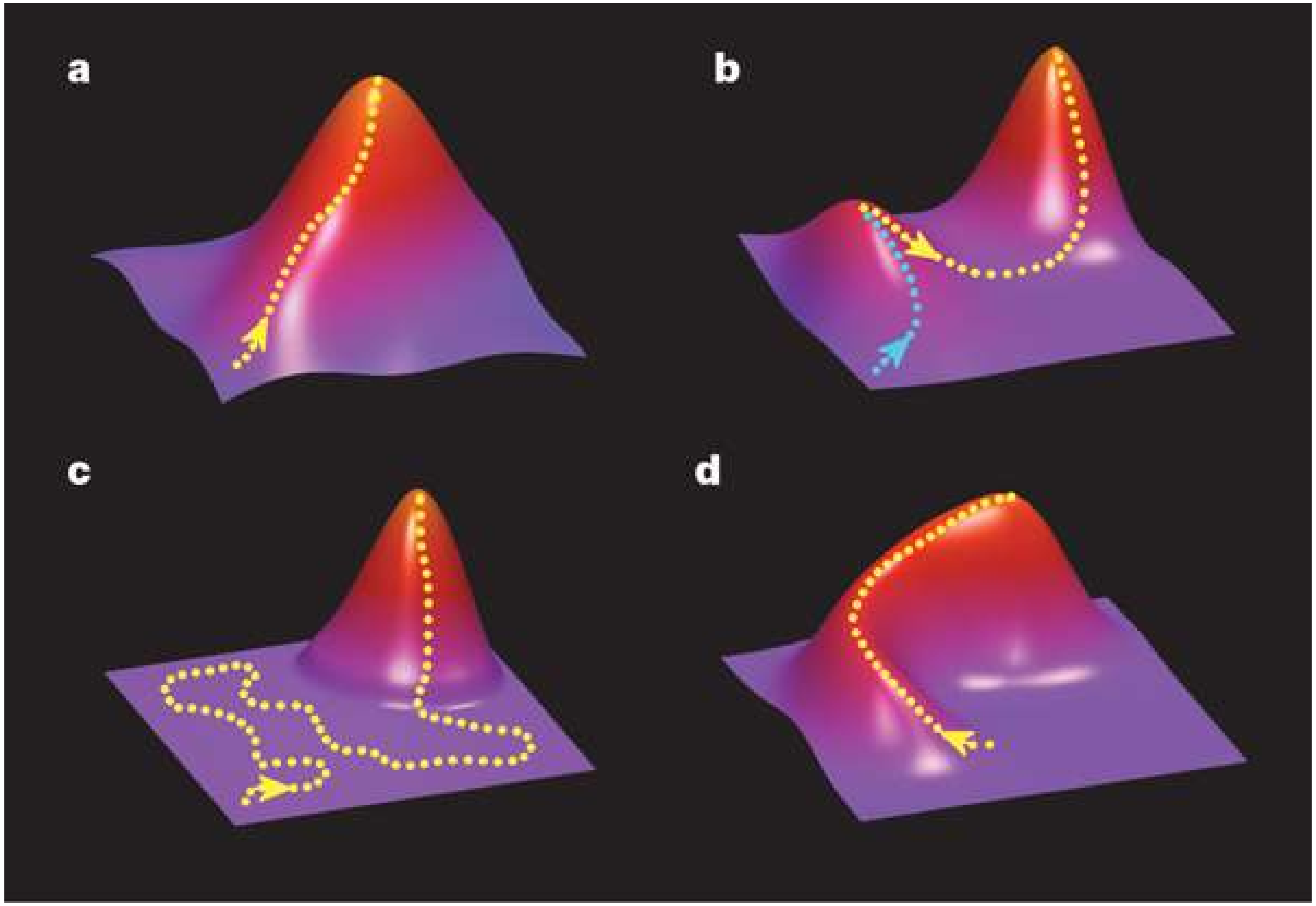
How likely are the paths?

Smooth
single
peak

rugged
multimodal

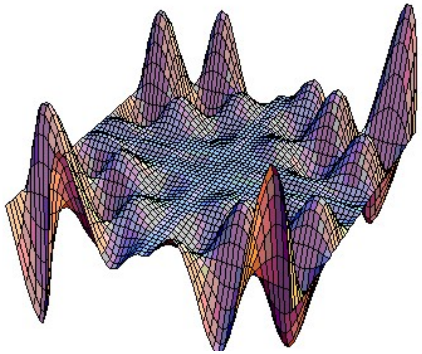
neutrality

detour



From Poelwijk et al. 2007

Landscape measures: How likely are evolutionary paths?



Generally: Fitness landscape

Geometrical object with features as

→ Number
→ Size
→ Form
→ Scattering

In terms of an optimization problem

→ Number of optima } Easy to measure

→ Distribution in search space
→ Nature of the space between them } Rather difficult to measure