

# The evolution of human cooperation: homophily, non-additive benefits, and higher-order relatedness

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# Acknowledgements

## Country:

I acknowledge the Turrbal and Yugara people and as the owners of this land. I pay respect to their Elders, past and present, and recognise QUT has always been a place of teaching, learning, and research.

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# Humans are cooperative

- Introspection — ‘I am a moral being’
- Humans are a highly cooperative species
- Eusocial insects – relatives
- Humans – cooperate with non-relatives, strangers



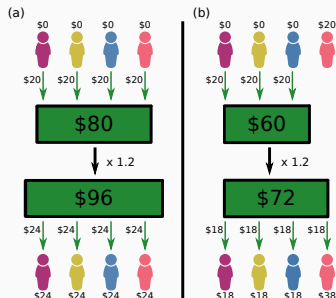
# Why cooperate?

- Cooperate = help others at a cost to yourself
- Why help others at a cost to yourself?
- Seems to violate Darwinian logic
- Tricky to think about costs and benefits
  - So others will help you in the future?
  - So you'll get a good reputation?
- Game theory: put cooperation problem in its purest form so we can think about it clearly



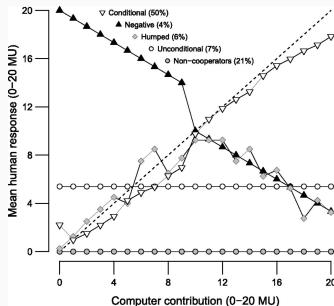
# Public goods game example

- Example:
  1. Public good that multiplies contributions by 1.2
  2. Everyone contributes  $\rightarrow$  maximise total payoffs
  3. However, not contributing maximises individual payoff
- Never makes sense to contribute
  - Returns are split equally
  - Marginal per-capita return =  $1.2/4 = 0.3 < 1$ 
    - 30c return for every \$1 contributed



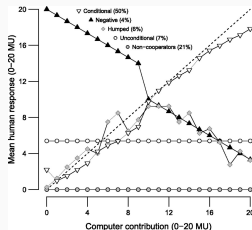
# How do people really behave in linear PGGs?

- Example: Burton-Chellew *et al.* (2016, PNAS)
  - Elicited contributions in PGG
  - Played against a computer
  - Computer play presumably removed fairness/empathy considerations
- Contribution level depends on contribution of others
- Similar results in other studies
- People genuinely seem believe this is payoff maximising!



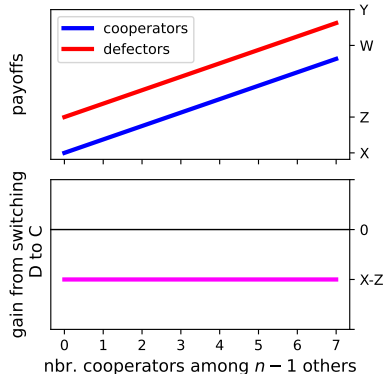
# Why do people make this mistake?

- Deeply unnatural scenario
- Previous work has focused on two 'mistakes':
  1. Mistake one-shot game for iterated game
  2. Mistake anonymous game for one with reputation concerns



My focus: Mistaking a linear game for a nonlinear one

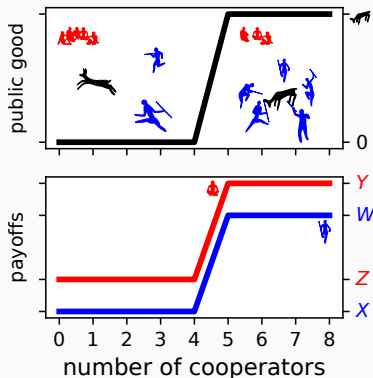
- In a linear game:
  - Benefit increases at constant rate with nbr. cooperators
  - No matter how many cooperators in the group, always lose by switching from D to C
- $n$ -player generalisation of the Prisoner's Dilemma





# Nonlinear public goods game

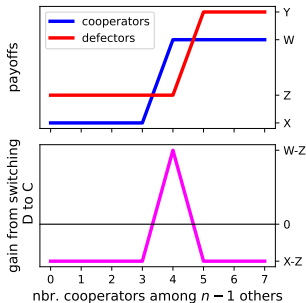
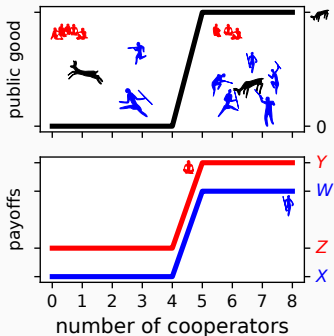
Claim: sigmoid benefit functions relevant to our early history



Note, defectors still get higher payoffs than Cooperators, but we need to think about it from the perspective of an individual decision-maker.

## Nonlinear public goods game (2)

Switching from defect to cooperate gains you the amount in pink.



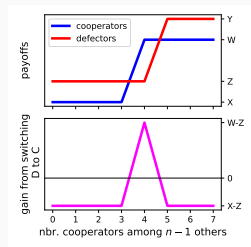
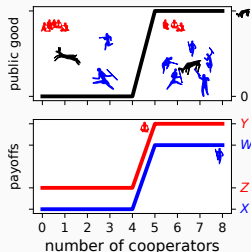
If the tribe is one short of the threshold, you should cooperate.

Depends on your chance to be the 'pivotal' player:

- if cooperators rare, don't cooperate
- if cooperators more common, might make sense to cooperate

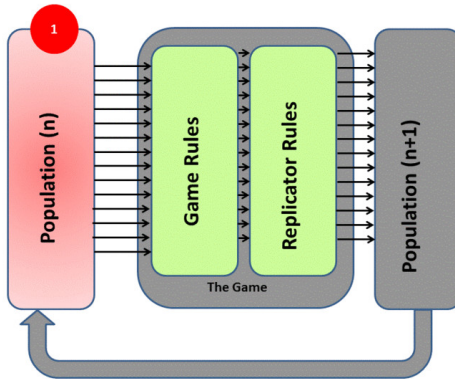
# Nonlinear public goods game: evolutionary perspective

- Game-theoretic perspective:
  - if cooperators rare: defect
  - if cooperators more common: maybe cooperate
- Translate game-theoretic to evolutionary perspective:
  - gene (or meme) encoding strategy
  - higher payoffs  $\rightarrow$  higher reproduction
- Evolutionary perspective:
  - if cooperators rare (invasion), cooperation can't succeed
  - if cooperators common, cooperation might persist



# Replicator dynamics overview

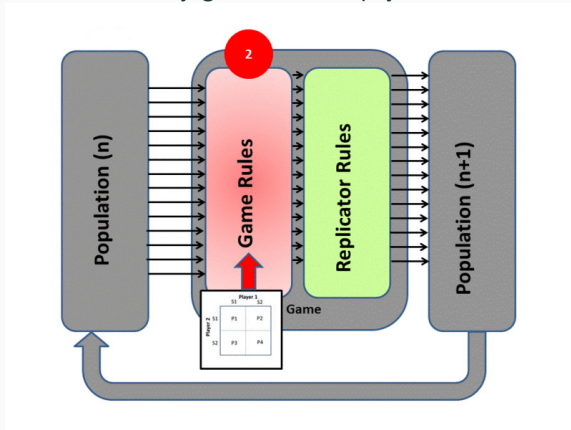
Population with genetically-encoded strategy (e.g., cooperate/defect)



(HowieKor, Creative Commons)

# Replicator dynamics overview

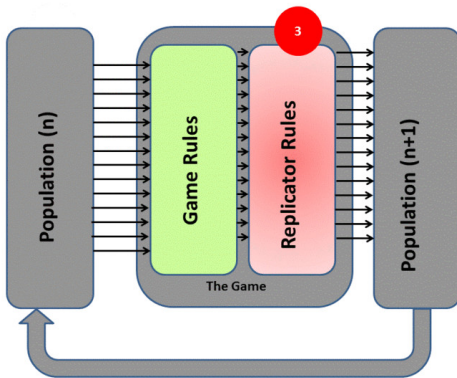
Play game, receive payoffs



(HowieKor, Creative Commons)

# Replicator dynamics overview

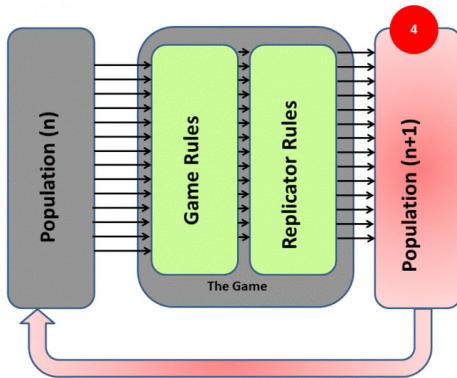
High payoffs  $\rightarrow$  more offspring



(HowieKor, Creative Commons)

# Replicator dynamics overview

New strategy frequencies in population



(HowieKor, Creative Commons)

# Replicator dynamics

Change in proportion of  $x$ -strategists:

The diagram shows the replicator equation  $\dot{p}_x = p_x \left( \bar{\pi}_x - \sum_{i=1}^m p_i \bar{\pi}_i \right)$  with several annotations:

- A blue arrow points from the text "expected payoff to  $x$ -strategists" to the  $\bar{\pi}_x$  term in the equation.
- A blue arrow points from the text "proportion of  $x$ -strategists" to the  $p_x$  term in the equation.
- A green arrow points from the text " $m$  is nbr. strategies" to the  $m$  in the summation index.
- A blue arrow points from the text "expected payoff in population" to the summation term  $\sum_{i=1}^m p_i \bar{\pi}_i$ .

$$\dot{p}_x = p_x \left( \bar{\pi}_x - \sum_{i=1}^m p_i \bar{\pi}_i \right)$$

- growth rate proportional to how much better  $x$ -strategists' payoffs are compared to average

Can also apply to cultural learning:

- I will talk in terms of genes and reproduction
- Exact same maths if you want to model ideas and social learning



# Replicator dynamics when groups formed randomly

expected payoff to x-strategists

$$\dot{p}_x = p_x \left( \bar{\pi}_x - \sum_{i=1}^m p_i \bar{\pi}_i \right)$$

- $e_x$ : indicator, focal plays strategy  $x$  (below: 1 when cooperator)
- $g_{nf}$ : non-focal strategy distribution (below: nbr. cooperators among nonfocals)

For prehistoric-hunt game:

$C$ 's payoff when  $g_{nf}$  non-focals are  $C$

prob.  $g_{nf}$  non-focals are  $C$

$$\begin{aligned} \bar{\pi}_C &= \sum_{g_{nf}=0}^{n-1} \pi(e_C, g_{nf}) \mathbb{P}[G_{nf} = g_{nf}], & \text{binomial} \\ &= \sum_{g_{nf}=0}^{n-1} \pi(e_C, g_{nf}) \binom{n-1}{g_{nf}} p_C^{g_{nf}} (1 - p_C)^{n-1-g_{nf}} \end{aligned}$$

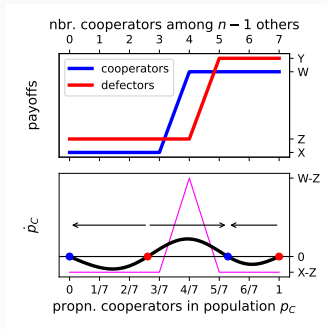
# Two main results about nonlinear games

*Recommended: Peña et al. (2014, J Theor Biol)*

Two main known results:

1. Cooperation can be sustained
  - Do people 'mistake' linear games for a nonlinear ones?
2. But cooperation cannot invade
  - Imagine a small nbr. of cooperators invading defectors...

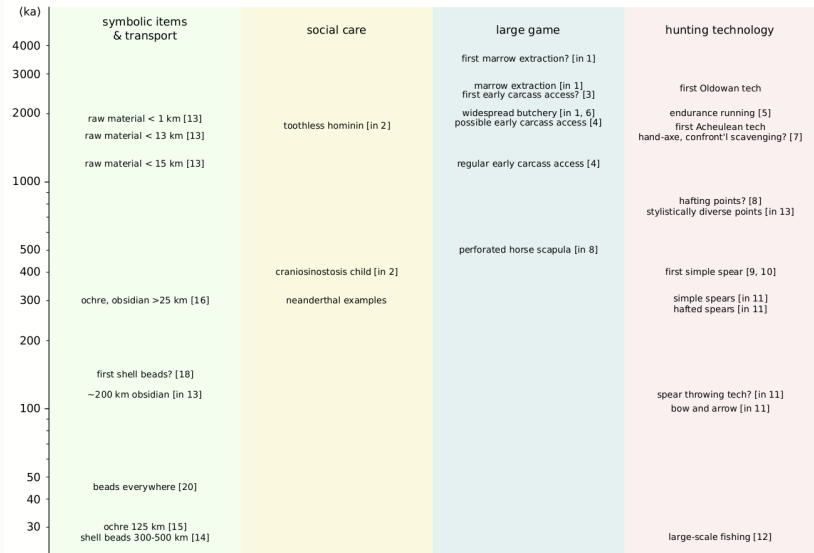
So how did cooperation even get started?



What if, instead of randomly formed groups, groups tend to form with family members? Then invading Cooperators more likely to be grouped with other Cooperators.

# Claim: Interactions with family more frequent in the past

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# Genetically homophilic group formation

colours = strategies; vertical lines divide families

## Random group formation

- Infinite population, no members from the same family



- Each strategy a random draw from the population



# Genetically homophilic group formation

colours = strategies; vertical lines divide families

## Random group formation

- Infinite population, no members from the same family



- Each strategy a random draw from the population



## Homophilic group formation

- Individuals prefer to group with family members



- Members in the same family have the same strategy



- Rare invading Cooperators grouped with other Cooperators

# Replicator dynamics with homophilic group formation

$$\dot{p}_x = p_x \left( \bar{\pi}_x - \sum_{i=1}^m p_i \bar{\pi}_i \right)$$

expected payoff to x-strategists (points to  $\bar{\pi}_x$ )  
 proportion of x-strategists (points to  $p_x$ )  
 expected payoff in population (points to  $\sum_{i=1}^m p_i \bar{\pi}_i$ )

but now expected payoff:

$$\bar{\pi}_C = \sum_{g_{nf}=0}^{n-1} \pi(e_C, g_{nf}) \mathbb{P}[G_{nf} = g_{nf} \mid G_0 = e_C]$$

no longer binomial (points to the probability term)  
 nonfocal strategy distribution depends on focal's strategy (points to the probability term)



# Hisashi's equation

Ohtsuki (2014, Phil Trans R Soc):

$$\dot{p}_1 = \sum_{g_{\text{nf}}=0}^{n-1} \sum_{\ell=g_{\text{nf}}}^{n-1} (-1)^{\ell-g_{\text{nf}}} \binom{\ell}{g_{\text{nf}}} \binom{n-1}{\ell}$$

relatedness terms

$$\left[ (1 - \rho_1) \rho_{\ell+1} \pi(e_1, g_{\text{nf}}) - \rho_1 (\rho_{\ell} - \rho_{\ell+1} \pi(e_2, g_{\text{nf}})) \right]$$

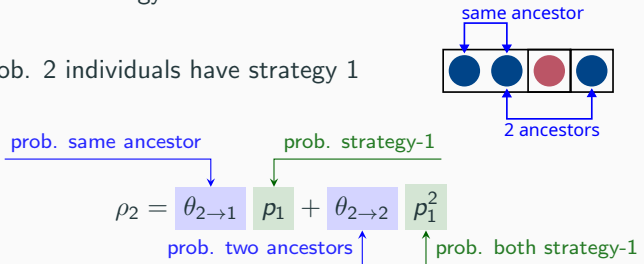
payoff terms

$\rho_{\ell}$ : probability that  $\ell$  players sampled from the group without replacement have strategy 1.

# Higher-order relatedness $\theta_{l \rightarrow m}$

$\rho_\ell$ : probability that  $\ell$  players sampled from the group without replacement have strategy 1.

e.g.,  $\rho_2$ : prob. 2 individuals have strategy 1



In general:

$$\rho_\ell = \sum_{m=1}^{\ell} \theta_{\ell \rightarrow m} p_1^m$$

Annotations for the general formula:

- sum over nbr. ancestors  $m$  (points to the summation index  $m$ )
- prob.  $\ell$  sampled have  $m$  common ancestors (points to  $\theta_{\ell \rightarrow m}$ )
- propn. strategy-1 in populatn (points to  $p_1$ )



# Linear PGG is a function of dyadic relatedness $\theta_{2 \rightarrow 1}$ only

- If the PGG is linear, then only need dyadic relatedness (many papers)

$$\dot{p}_1 = f(\theta_{2 \rightarrow 1})$$

dyadic relatedness, Hamilton's  $r$  ↑

- because the  $n$ -player game payoff can be written as a sum of payoffs in 2-player games

$$\pi^{(n)}(e_x, g_{\text{nf}}^{(n)}) \equiv \sum_{g_{\text{nf}}^{(2)}} \pi^{(2)}(e_x, g_{\text{nf}}^{(2)})$$

- However, if the payoff function is nonlinear, higher-order relatedness coefficients needed (e.g.,  $\theta_{3 \rightarrow 1}$ ,  $\theta_{3 \rightarrow 2}$ ,  $\theta_{4 \rightarrow 1}$ , etc.)
- How to get them?

# How do we calculate the higher-order relatedness terms?

From the probabilities  $F_q$  of each group family-size distribution  $q$ !

Example: Given each family-size distribution  $q$ , calculate  $\theta_{2 \rightarrow 1}$ .

|                 | partition $q$                                                                     | $\theta_{2 \rightarrow 1} \mid q$              | explanation                           |
|-----------------|-----------------------------------------------------------------------------------|------------------------------------------------|---------------------------------------|
| $F_{[4]}$       |  | 1                                              | Any 2 will have a common ancestor.    |
| $F_{[3,1]}$     |  | $\frac{3}{4} \times \frac{2}{3} = \frac{1}{2}$ | Both must be blue (family size 3).    |
| $F_{[2,2]}$     |  | $1 \times \frac{1}{3} = \frac{1}{3}$           | Choose any, then its 1 family member. |
| $F_{[2,1,1]}$   |  | $\frac{2}{4} \times \frac{1}{3} = \frac{1}{6}$ | Only possible in the partition of 2.  |
| $F_{[1,1,1,1]}$ |  | 0                                              | Not possible.                         |

So if we can calculate all  $F_q$ , we can calculate all  $\theta_{l \rightarrow m}$  and solve the dynamics.

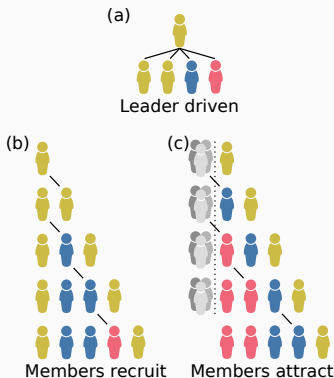
# Homophilic group-formation models

(a) Leader driven:

- The leader is chosen at random from the population.
- Leader recruits/attracts kin with probability  $h$  and nonkin with probability  $1 - h$ .
- Group family size distribution

$$F_{[\ell, 1, \dots, 1]} = \binom{n-1}{\ell-1} h^{\ell-1} (1-h)^{n-\ell}.$$

$h$  =: genetic homophily



# Homophilic group-formation models

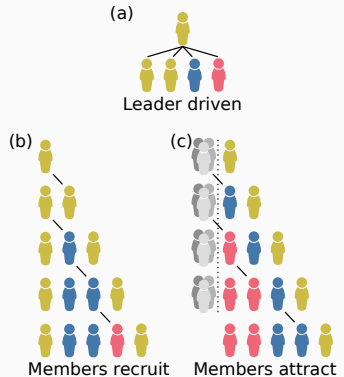
(b) Members recruit:

- All group members have an equal chance to recruit the next member.
- Equation in Kristensen *et al.* (2022)

(c) Members attract:

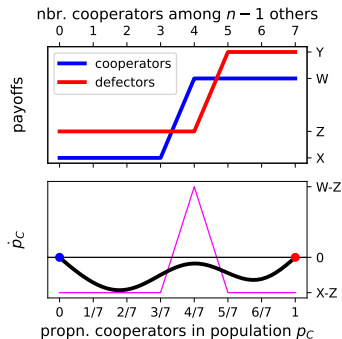
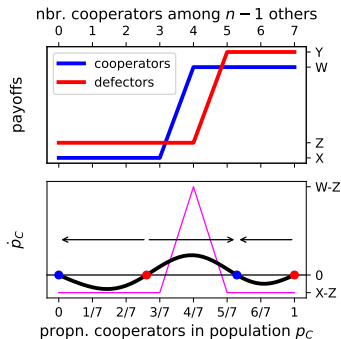
- Outsiders attracted to kin
- But also attracted to the group as a whole
- Use Ewens' formula (Ewen 1972).

$h$  =: genetic homophily



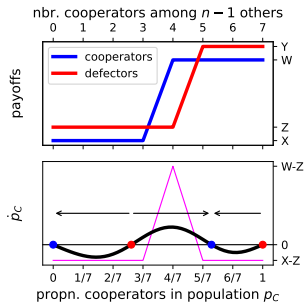
NOTE: can be interpreted in terms of 'matching rules' (*sensu* Jensen & Rigos, 2018, Int J Game Theory), i.e., strategy homophily, selecting someone with the same strategy or making a 'mistake'

Recall no-homophily result: cooperation can (sometimes) persist but it can never invade:

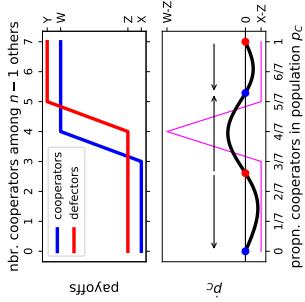


We want to go backwards in time — increase homophily — and see if cooperation can invade.

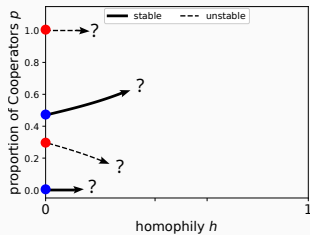
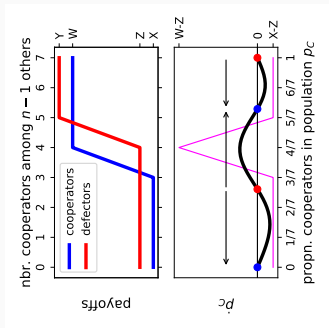
# Results



# Results



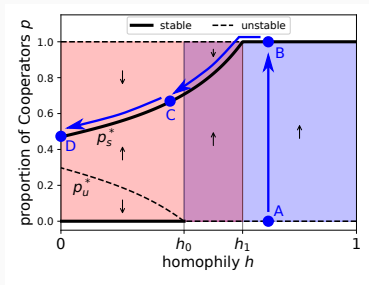
# Results





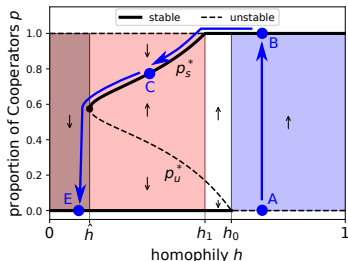
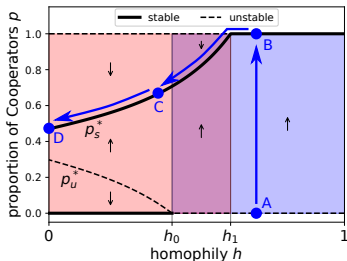
# Results

- Cooperation cannot invade a threshold game with random group formation
  - Also true for sigmoid games in general (Peña *et al.*, 2014)
- But can arise through historical homophily



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  - Also true for sigmoid games in general (Peña *et al.*, 2014)
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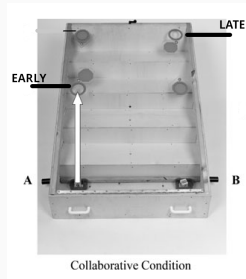
- For cooperation to persist, either:
  - Parameters such that it can be sustained in a well-mixed population
  - Some degree of homophily maintained

# Many discrete strategies

- So far, 2 strategies; natural extension,  $m$  strategies
- Discrete strategies:
  - I could have modelled cooperate and defect as *degree* of cooperation — one continuous strategy
  - However, some strategies are naturally discrete
    - e.g., conditioning on the actions of others
  - Shared intentionality (Genty et al., 2020; Tomasello, 2020):
    - form a collective 'we' with a jointly optimised goal
    - make a joint commitment (!?) to the goal
    - coordinate our actions towards achieving it

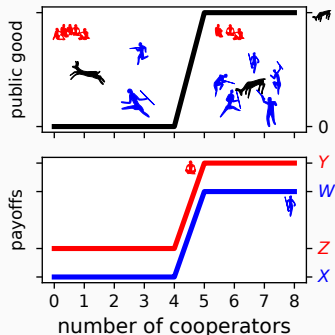
# Commitment

- Commitment is a norm: one should do what one promised
- Commitment distinguishes us from other apes
  - Experimental situations where one individual receives their reward early
  - 3.5-year-old children continue contributing until their partner also gets their reward (Hamann et al., 2012)
  - chimpanzees don't distinguish between continuing to help in an existing collaboration versus starting a new one (Greenberg et al., 2010)

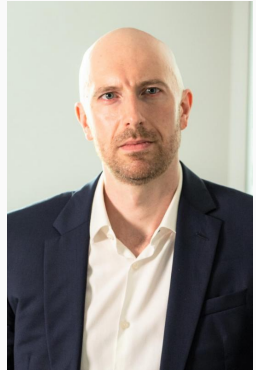


# Commitment and coordination

- In the threshold game, hunters are a bit stupid
  - Cooperator will run off to do the hunt by themselves
- But people don't really behave this way; they coordinate
  - If we were in this situation, we'd have a conversation
  - That's also how people behave experimentally
    - e.g., Van de Kragt *et al.* (1983, *Am Pol Sci Rev*)
- Plus, coordination improves the evolutionary prospects for cooperation!



- Newton (2017 Games Econ Behav)  
'shared intentionality' evolves under  
fairly general conditions in a public  
goods game

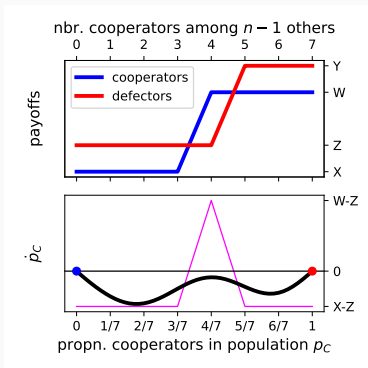


Jonathan Newton  
Kyoto Uni

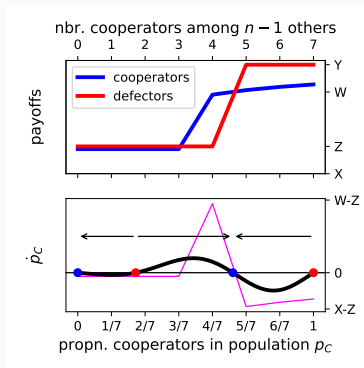
# Coordination in a threshold-game example

- Extend the threshold game:
  - Coordinating cooperators draw straws to decide who will contribute
  - The ability to coordinate entails a small cognitive cost  $\varepsilon$

old threshold game

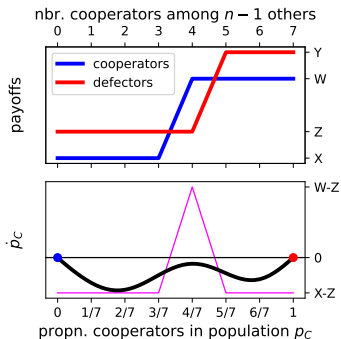


coordinated cooperation game

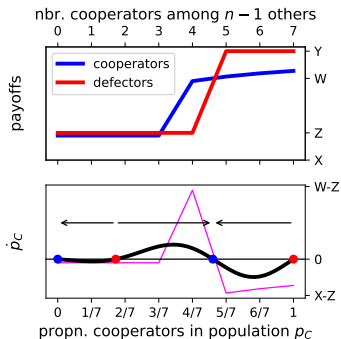


# Coordination in a threshold game example

old threshold game



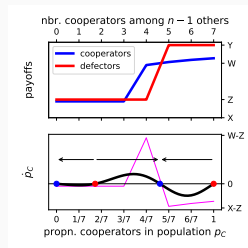
coordinated cooperation game



- Sustains cooperation where it could not otherwise be sustained
- Can't invade, but we already know we can overcome this with homophily



- Coordination improves the prospects for coordination
- Newton: Coordination can even sustain cooperation in a linear game!
- ... wait
  - It never makes sense to contribute in the linear game
  - It's true the Defectors can't invade, but what about a type who participates in the lottery but doesn't follow through?
- Need to include another new strategy: Liars



## New notation

- Subscripts: 0 = focal player; nf = nonfocal players; a = all players
- $\mathbf{G}$  random variable for strategy composition, takes values  $\mathbf{g}$



- Players:  $\mathbf{g}_0 = (0, 1, 0, 0)$ ,  $\mathbf{g}_1 = (1, 0, 0, 0)$ ,  $\mathbf{g}_2 = (0, 0, 0, 1), \dots$
- Whole-group:  $\mathbf{g}_a = (3, 2, 0, 1)$
- Nonfocal:  $\mathbf{g}_{nf} = (3, 1, 0, 1)$
- $\mathbf{g}_j = \mathbf{e}_x$ : player  $j$  plays strategy  $s_x$  (a 1 in the  $x$ -th position)

# Many strategies

How does a trait change frequency over time?



George Robert Price

dynamics of propn. of  $s_x$

$$\Delta p_x = \text{Cov}[G_{0,x}, W_0],$$

focal's strategy indicator      fitness of focal

$$G_{0,x} = \begin{cases} 1 & \text{if focal strategy } s_x, \\ 0 & \text{otherwise.} \end{cases}$$

# Many strategies

dynamics of propn. of  $s_x$

$$\Delta p_x = \text{Cov}[G_{0,x}, W_0],$$

1 if focal plays  $s_x$ ; 0 otherwise      fitness of focal

selection strength      focal payoff random variable

$$W_0 = \underbrace{s}_{\text{survival probability}} + \overbrace{(1-s)}^{\text{vacancies}} \frac{1 + \delta \Pi_0}{1 + \delta \bar{\pi}}$$

avg. payoff in population

Useful identity:  $\text{Cov}[X, aY + b] = a \text{Cov}[X, Y]$

Substituting and rearranging:

strategy indicator      focal payoff

$$\Delta p_x \propto \text{Cov}[G_{0,x}, \Pi_0]$$

# Other member accounting

$$\Delta p_x \propto \text{Cov} \left[ \overset{\text{focal's strategy indicator}}{G_{0,x}}, \overset{\text{focal payoff}}{\Pi_0} \right]$$

Payoff to the focal individual:

$$\Pi_0 = \sum_{i=1}^m \overset{\text{1 if focal plays } s_i; \text{ 0 otherwise}}{G_{0,i}} \overset{\text{payoff to } s_i\text{-player}}{\pi(e_i, \overset{\text{nonfocal strategy composition}}{G_{\text{nf}}})}$$

Useful identity:  $\text{Cov}[X, Y] = \mathbb{E}[XY] - \mathbb{E}[X] \mathbb{E}[Y]$

$$\Delta p_x = \mathbb{E} \left[ \overset{\text{nonfocal strategy composition}}{G_{0,x}} \pi(e_x, \overset{\text{nonfocal strategy composition}}{G_{\text{nf}}}) \right] - p_x \sum_{i=1}^m \mathbb{E} \left[ G_{0,i} \pi(e_i, \overset{\text{nonfocal strategy composition}}{G_{\text{nf}}}) \right]$$

nonfocal strategy composition

$$\Delta p_x = \mathbb{E} \left[ G_{0,x} \pi(e_x, \mathbf{G}_{\text{nf}}) \right] - p_x \sum_{i=1}^m \mathbb{E} \left[ G_{0,i} \pi(e_i, \mathbf{G}_{\text{nf}}) \right]$$

Let  $\mathcal{G}_{\text{nf}}$  be the set of all strat. compositions  $\mathbf{g}_{\text{nf}}$ . Then expectations:

$$\begin{aligned} \mathbb{E} [G_{0,i} \pi(e_i, \mathbf{G}_{\text{nf}})] &= \sum_{\mathbf{g}_{\text{nf}} \in \mathcal{G}_{\text{nf}}} \pi(e_i, \mathbf{g}_{\text{nf}}) \mathbb{P}[\mathbf{G}_0 = e_i, \mathbf{G}_{\text{nf}} = \mathbf{g}_{\text{nf}}] \\ &= \sum_{\mathbf{g}_{\text{nf}} \in \mathcal{G}_{\text{nf}}} \pi(e_i, \mathbf{g}_{\text{nf}}) \underbrace{\mathbb{P}[\mathbf{G}_0 = e_i]}_{p_i} \mathbb{P}[\mathbf{G}_{\text{nf}} = \mathbf{g}_{\text{nf}} \mid \mathbf{G}_0 = e_i] \\ &= p_i \underbrace{\sum_{\mathbf{g}_{\text{nf}} \in \mathcal{G}_{\text{nf}}} \pi(e_i, \mathbf{g}_{\text{nf}}) \mathbb{P}[\mathbf{G}_{\text{nf}} = \mathbf{g}_{\text{nf}} \mid \mathbf{G}_0 = e_i]}_{\bar{\pi}_i} \end{aligned}$$

Recovered replicator eqn:  $\Delta p_x \propto p_x \left( \bar{\pi}_x - \sum_{i=1}^m p_i \bar{\pi}_i \right) = p_x (\bar{\pi}_x - \bar{\pi})$ .

But  $\mathbb{P}[\mathbf{G}_{\text{nf}} = \mathbf{g}_{\text{nf}} \mid \mathbf{G}_0 = e_i]$  is not obvious: 

Idea: draw a group at random, then draw a focal individual.

$$\Delta p_x \propto \text{Cov} \left[ \overset{\text{strategy indicator}}{G_{0,x}}, \overset{\text{focal payoff}}{\Pi_0} \right]$$

This time, focus on the whole-group distribution.

new payoff fnc wrt whole-group strategy composition

$$\Pi_0 = \sum_{i=1}^m G_{0,i} \hat{\pi}(\mathbf{e}_i, \mathbf{G}_a)$$

Using a similar method to before involving covariance identities and re-arranging, we obtain

$$\Delta p_x = \sum_{\mathbf{g}_a \in \mathcal{G}_a} \left( \frac{g_{a,x}}{n} \hat{\pi}(\mathbf{e}_x, \mathbf{g}_a) - p_x \sum_{i=1}^m \frac{g_{a,i}}{n} \hat{\pi}(\mathbf{e}_i, \mathbf{g}_a) \right) \mathbb{P}[\mathbf{G}_a = \mathbf{g}_a]$$

prob. of whole-group strategy composition

## Prob. of whole-group strategy composition, $\mathbb{P}[G_a = g_a] = ?$

colours = strategies; vertical lines divide families

$$\mathbb{P}[G_a = \boxed{\bullet \bullet \bullet \bullet \bullet \bullet}]$$



# Prob. of whole-group strategy composition, $\mathbb{P}[G_a = g_a] = ?$

colours = strategies; vertical lines divide families

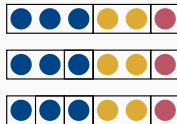
$$\mathbb{P}[G_a = \boxed{\text{blue} \text{ blue} \text{ blue} \text{ yellow} \text{ yellow} \text{ pink}}]$$



# Prob. of whole-group strategy composition, $\mathbb{P}[G_a = g_a] = ?$

colours = strategies; vertical lines divide families

$$\mathbb{P}[G_a = \boxed{\text{blue} \text{ blue} \text{ blue} \text{ yellow} \text{ yellow} \text{ pink}}]$$

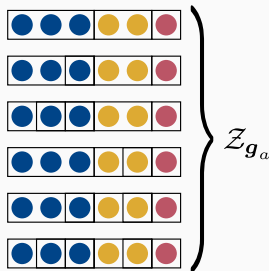


# Prob. of whole-group strategy composition, $\mathbb{P}[G_a = g_a] = ?$

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$$\mathbb{P}[G_a = \boxed{\text{blue} \text{ blue} \text{ blue} \text{ yellow} \text{ yellow} \text{ pink}}]$$

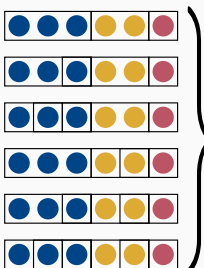
$$= \sum_{z \in \mathcal{Z}_{g_a}} \mathbb{P}[Z = z]$$



# Prob. of whole-group strategy composition, $\mathbb{P}[G_a = g_a] = ?$

colours = strategies; vertical lines divide families

$$\begin{aligned}
 & \mathbb{P}[G_a = \boxed{\text{blue} \text{ blue} \text{ blue} \text{ yellow} \text{ yellow} \text{ pink}}] \\
 &= \sum_{z \in \mathcal{Z}_{g_a}} \mathbb{P}[Z = z]
 \end{aligned}$$



$\mathcal{Z}_{g_a}$

$$\begin{aligned}
 & \mathbb{P}[Z = \boxed{\text{blue} \text{ blue} \text{ blue} \text{ yellow} \text{ yellow} \text{ pink}}] \\
 &= \underbrace{\mathbb{P}[\boxed{\text{grey} \text{ grey} \text{ grey} \text{ grey} \text{ grey} \text{ grey}}]}_{F_y} \cdot \underbrace{\mathbb{P}[\boxed{\text{blue} \text{ blue} \text{ blue} \text{ yellow} \text{ yellow} \text{ pink}} \mid \boxed{\text{grey} \text{ grey} \text{ grey} \text{ grey} \text{ grey} \text{ grey}}]}_{C(z) \cdot A(z, p)}
 \end{aligned}$$

Probability of strategywise family-size distribution:

get from homophilic group-formation model

$$\mathbb{P}[\mathbf{G}_a = \mathbf{g}_a] = \sum_{\mathbf{z} \in \mathcal{Z}_{\mathbf{g}_a}} F_y \quad C(\mathbf{z}) \quad A(\mathbf{z}, \mathbf{p})$$

count of multiset permutations

prob. families' strategies

$$A(\mathbf{z}, \mathbf{p}) = \prod_{i=1}^m p_i^{\|z_i\|}$$

nbr. families pursuing strategy  $s_i$

Analogous to the power terms in 2-strategy game, e.g.,

$$\rho_2 = \theta_{2 \rightarrow 1} p_1 + \theta_{2 \rightarrow 2} p_1^2$$

# Whole-group accounting

Bringing it all together:

$$\Delta p_x \propto \sum_{\mathbf{g}_a \in \mathcal{G}_a} \left( \frac{\mathbf{g}_{a,x}}{n} \hat{\pi}(\mathbf{e}_x, \mathbf{g}_a) - p_x \sum_{i=1}^m \frac{\mathbf{g}_{a,i}}{n} \hat{\pi}(\mathbf{e}_i, \mathbf{g}_a) \right) \left( \sum_{\mathbf{z} \in \mathcal{Z}_{\mathbf{g}_a}} C(\mathbf{z}) A(\mathbf{z}, \mathbf{p}) F_{\text{sum}(\mathbf{z})} \right)$$

Diagram annotations:

- prob. focal pursues  $s_x$**  (pink arrow pointing to  $\frac{\mathbf{g}_{a,x}}{n}$ )
- over strategywise family-sizes** (green arrow pointing to  $\sum_{\mathbf{z} \in \mathcal{Z}_{\mathbf{g}_a}}$ )
- sum over group strategy compositions** (blue arrow pointing to  $\sum_{\mathbf{g}_a \in \mathcal{G}_a}$ )

- Not as intuitive as the traditional replicator equation
  - $\Delta p_x \propto p_x (\bar{\pi}_x - \bar{\pi})$
- Might be useful from computational perspective because we've split homophily calculations off from strategy identity
- Now it's clearer how to calculate  $\mathbb{P}[\mathbf{G}_{\text{nf}} = \mathbf{g}_{\text{nf}} \mid \mathbf{G}_0 = \mathbf{e}_i]$

- Idea: transform payoffs so they take into account homophily
- Well-mixed game:  $\dot{p}_i = p_i(\bar{\pi}_i - \bar{\pi}) = p_i((A \mathbf{p})_i - \mathbf{p}^T A \mathbf{p})$ , where  $a_{i,j} = \pi(\mathbf{e}_i, \mathbf{e}_j)$ ,

$$\bar{\pi} = \begin{pmatrix} \bar{\pi}_1 \\ \vdots \\ \bar{\pi}_m \end{pmatrix} = \begin{matrix} \xrightarrow{\text{nonfocal's strategy}} \\ \downarrow \text{focal's strat.} \end{matrix} \begin{pmatrix} a_{1,1} & \dots & a_{1,m} \\ \vdots & & \vdots \\ a_{m,1} & \dots & a_{m,m} \end{pmatrix} \begin{pmatrix} p_1 \\ \vdots \\ p_m \end{pmatrix} = \begin{pmatrix} a_{1,1}p_1 + \dots + a_{1,m}p_m \\ \vdots \\ a_{m,1}p_1 + \dots + a_{m,m}p_m \end{pmatrix}$$

- Now with homophily, dyadic relatedness  $\theta_{2 \rightarrow 1}$

$$B = \underbrace{(1 - \theta_{2 \rightarrow 1}) \begin{pmatrix} a_{1,1} & \dots & a_{1,m} \\ \vdots & & \vdots \\ a_{m,1} & \dots & a_{m,m} \end{pmatrix}}_{i \text{ matched with random with prob. } 1 - \theta_{2 \rightarrow 1}} + \underbrace{\theta_{2 \rightarrow 1} \begin{pmatrix} a_{1,1} & \dots & a_{1,1} \\ \vdots & & \vdots \\ a_{m,m} & \dots & a_{m,m} \end{pmatrix}}_{i \text{ matched with } i \text{ with prob. } \theta_{2 \rightarrow 1}}$$

- Dynamics of  $A$  with homophily  $\equiv$  dynamics of  $B$  well-mixed

$$\dot{p}_i = p_i((B \mathbf{p})_i - \mathbf{p}^T B \mathbf{p})$$

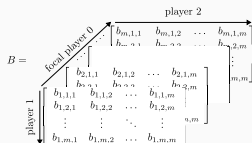
## Aside: Payoff transformation $n$ players

Seeking a solution to:

$$B = \begin{array}{c} \begin{array}{c} \text{player 1} \downarrow \end{array} \begin{array}{c} \begin{array}{c} \text{focal player 0} \nearrow \end{array} \begin{array}{c} \begin{array}{c} \vdots \\ \vdots \\ \vdots \end{array} \end{array} \end{array} \begin{array}{c} \begin{array}{c} \begin{array}{c} \begin{array}{c} \begin{array}{c} b_{1,1,1} \quad b_{1,1,2} \quad \dots \quad b_{1,1,m} \\ b_{1,2,1} \quad b_{1,2,2} \quad \dots \quad b_{1,2,m} \\ \vdots \quad \quad \quad \ddots \quad \quad \quad \vdots \\ b_{1,m,1} \quad b_{1,m,2} \quad \dots \quad b_{1,m,m} \end{array} \\ \vdots \\ \vdots \\ \vdots \end{array} \end{array} \end{array} \begin{array}{c} \begin{array}{c} \begin{array}{c} \begin{array}{c} b_{m,1,1} \quad b_{m,1,2} \quad \dots \quad b_{m,1,m} \\ b_{m,2,1} \quad b_{m,2,2} \quad \dots \quad b_{m,2,m} \\ \vdots \\ b_{m,m,1} \quad b_{m,m,2} \quad \dots \quad b_{m,m,m} \end{array} \end{array} \end{array} \end{array}$$



# Payoff transformation $n$ players



$$b_u = \sum_{q \vdash n} F_q \left( \sum_{q_0 \in q} \frac{q_0}{n |\mathcal{J}_{q_0, q}|} \left( \sum_{j \in \mathcal{J}_{q_0, q}} a_{u_j} \right) \right)$$

get from group-formation model

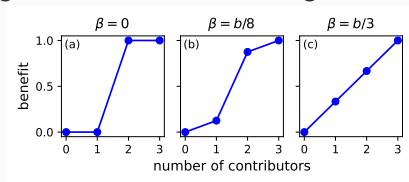
Code to calculate it on Github:

1. Numerically: TransmatBase class functions/transmat\_base.py.
2. Symbolically: functions/symbolic\_transformed.py.

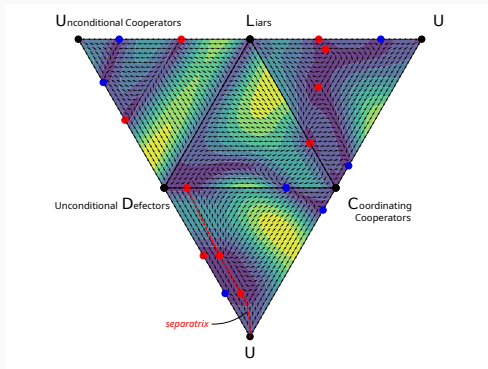
But why would you want to do this?

- $B$  is expensive to calculate, but matrix multiplication is optimised, can be worth the trade-off when finding steady states
- Use maths from well-mixed case, e.g., Jorge Peña's analysis techniques (example in appendix)

- Game with 4 strategies:
  1.  $D$ : unconditional Defector, never contributes
  2.  $C$ : Coordinating cooperator, hold lottery, follow through if chosen
    - Nbr. contributors  $\tau$  = threshold, or inflection point if sigmoid
  3.  $L$ : Liar, participate in lottery, never contributes
  4.  $U$ : Unconditional cooperator, always contributes
- $C$  and  $L$  pay cognitive cost  $\varepsilon$  regardless of game outcome
- $U$  and  $C$  pay contribution cost  $c$  if contributing
- Explore the range from linear to threshold game

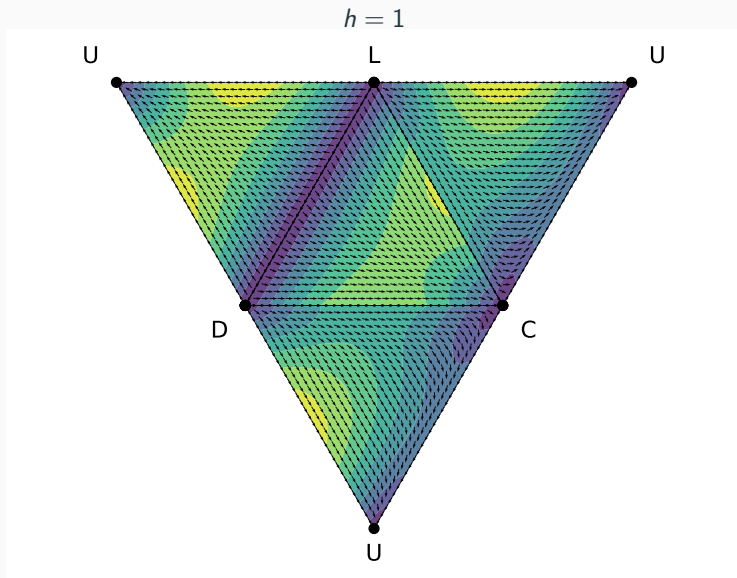


Example 3-player - symbolic analysis  
Example 8-player - numerical analysis

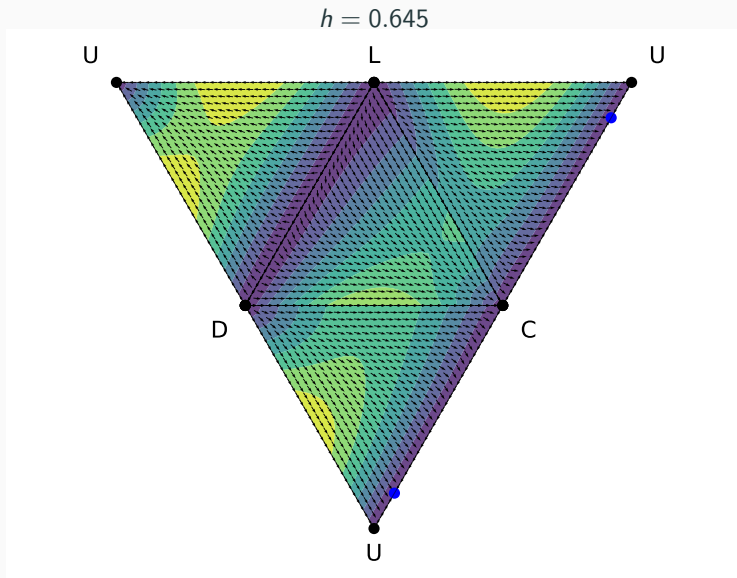


- Evolutionary dynamics for a given homophily level  $h$ 
  - Dynamics inside a triangular pyramid
  - The points represent a population with just one strategy, lines 2 strategies, triangles 3
  - Blue points are stable in that dimension, red points unstable

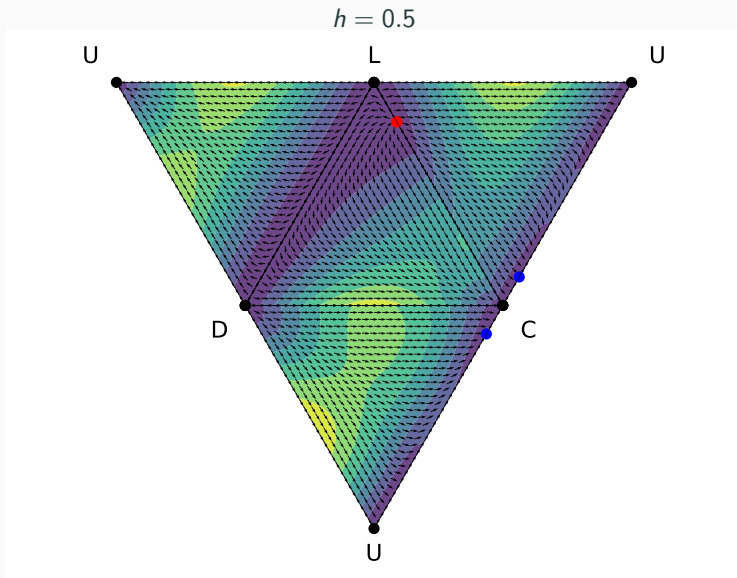
## Results 1: fairly nonlinear benefits function



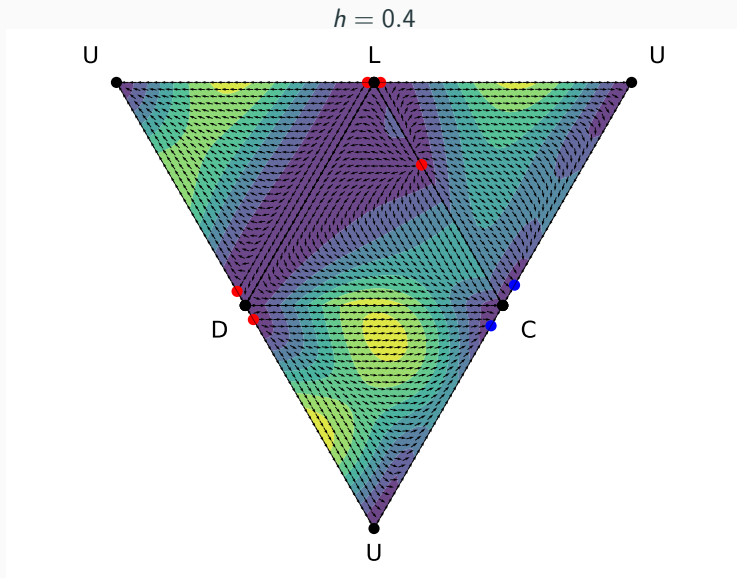
## Results 1: fairly nonlinear benefits function



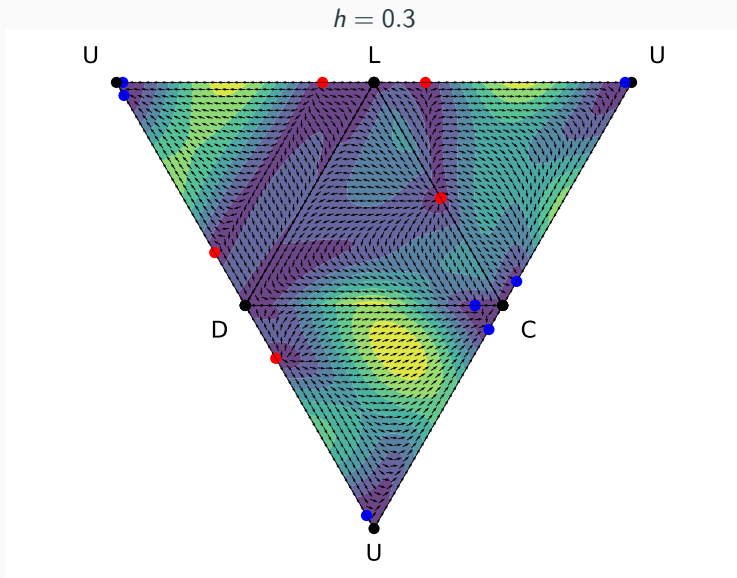
## Results 1: fairly nonlinear benefits function



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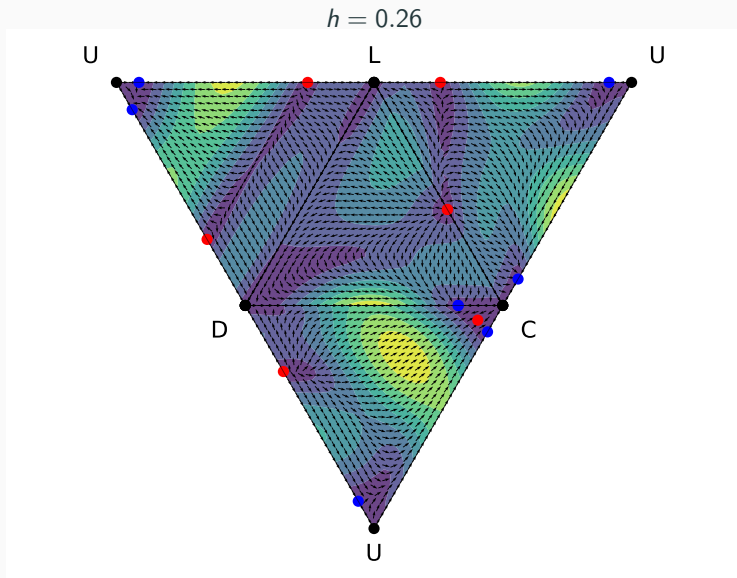


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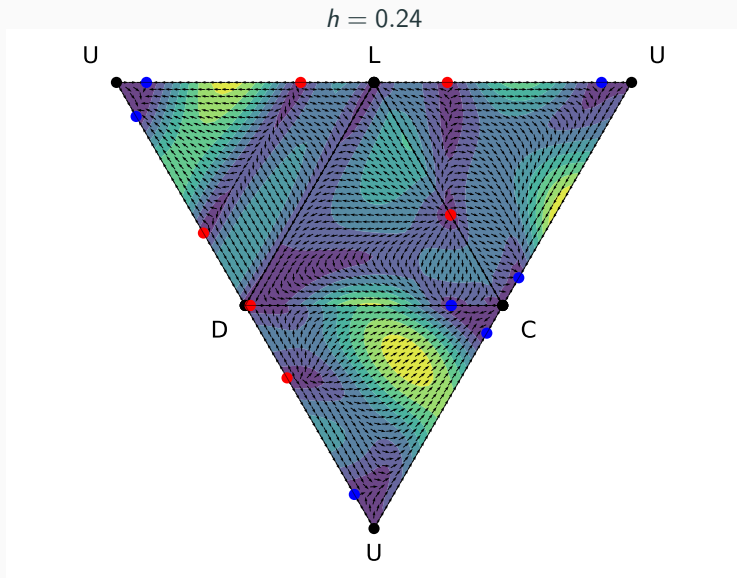




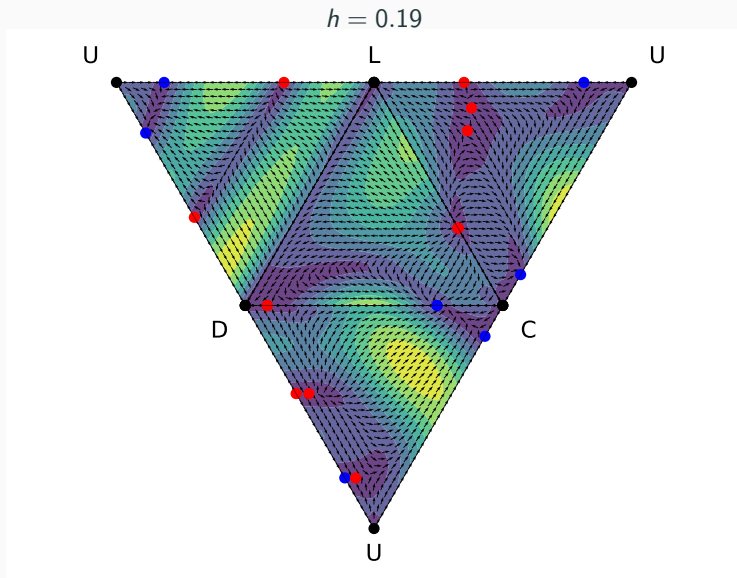
## Results 1: fairly nonlinear benefits function



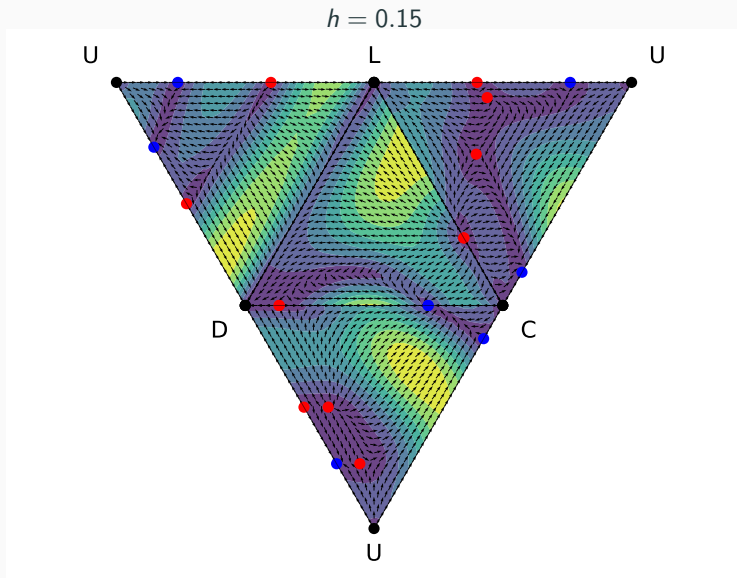
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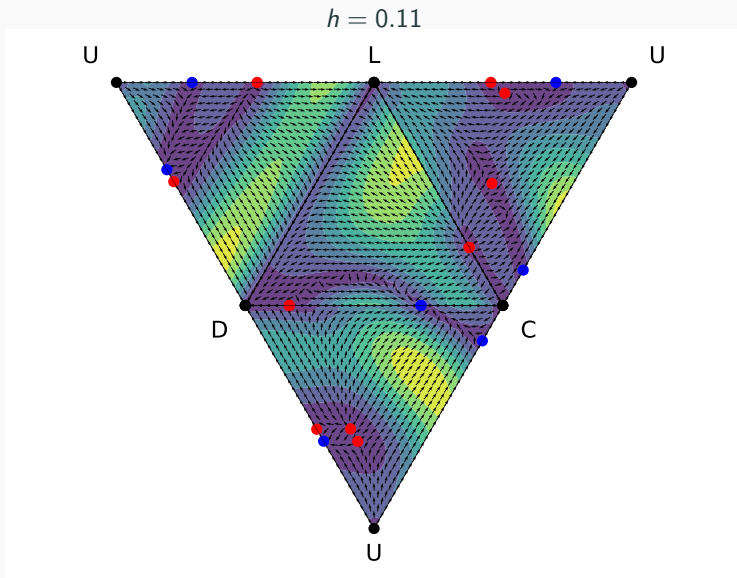
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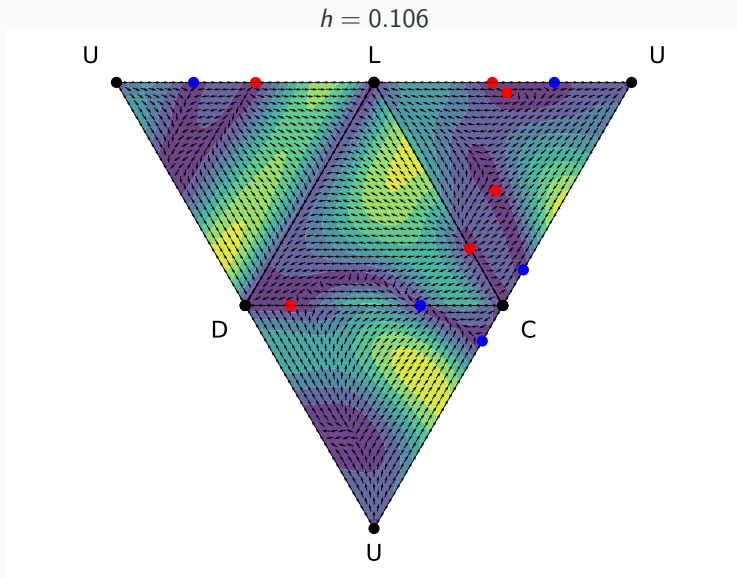
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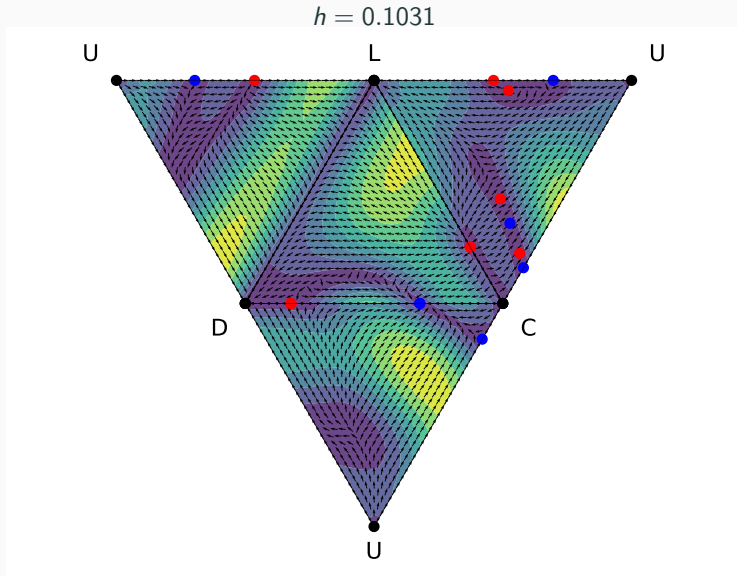
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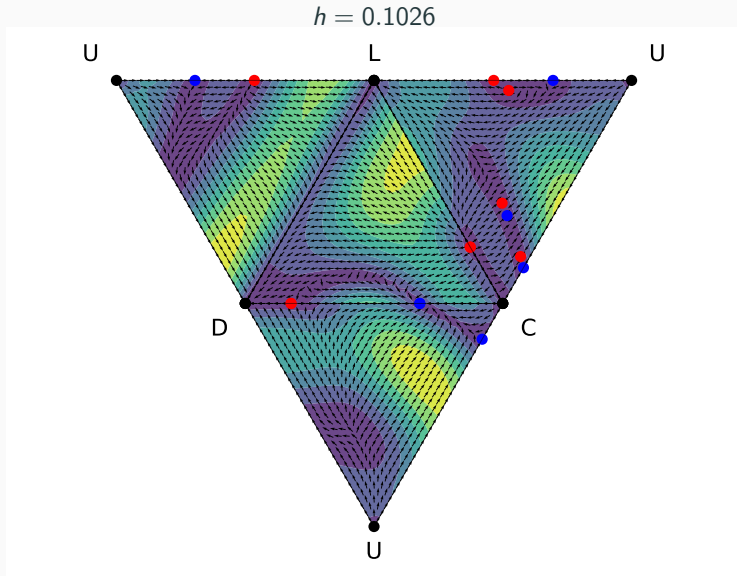
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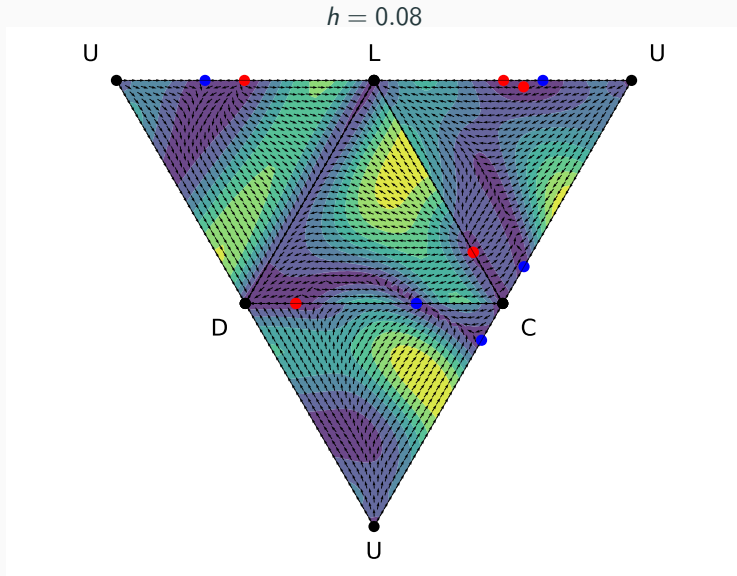


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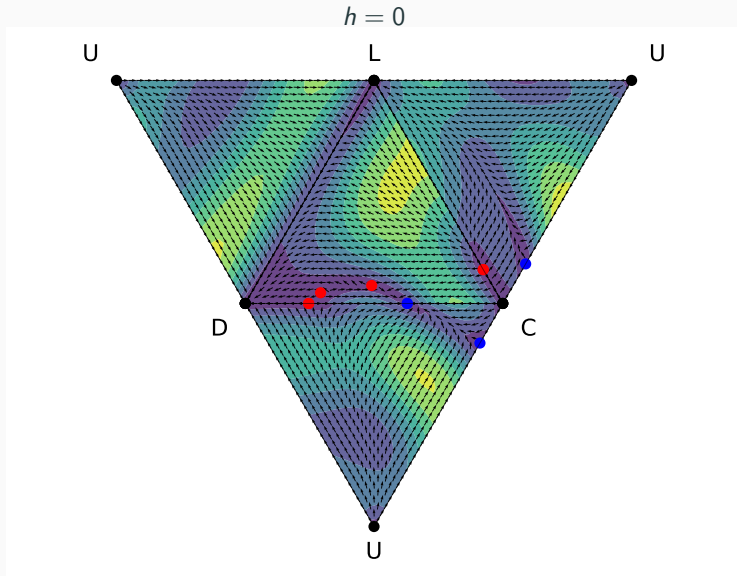


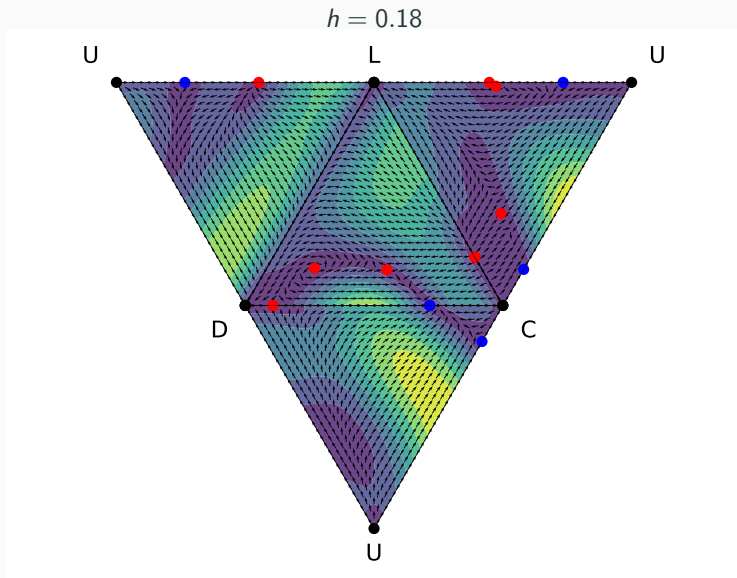


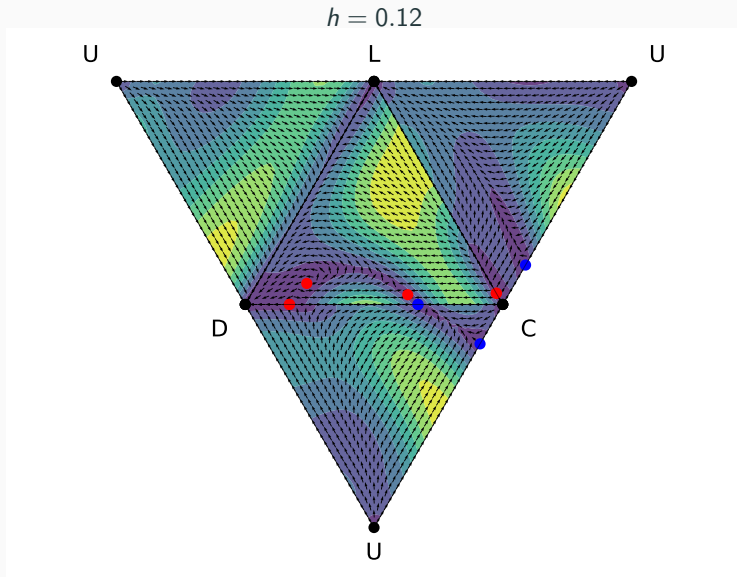
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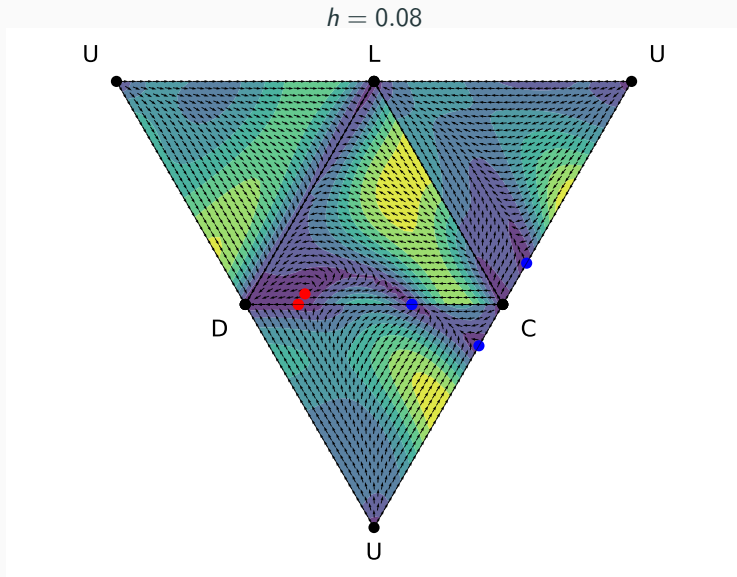


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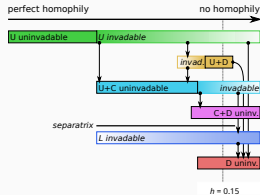




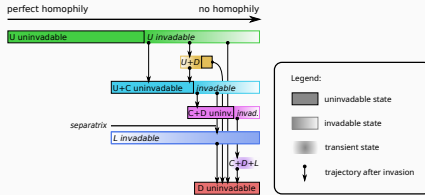


# Results summary

(a) more nonlinear



(b) more linear



## Results:

1. Coordination allows cooperation where it cannot otherwise persist
2. First arose through kin selection
3. To persist in modern scenario, either:
  - Keep some degree of homophily in modern interactions
  - Payoff function non-linear enough

# Talk summary

- Mathematical framework combines discrete-strategy group games with kin selection (or ‘matching rules’)
- Investigate: how cooperation first arose, and how it can persist

github.com/nadiahpk

nadiah.org

The screenshot shows the GitHub profile of Nadiah Kristensen (nadiahpk). The profile includes a bio, a list of repositories, a contribution graph, and a list of organizations. The bio states: "Models for ecology, evolution, and cooperation. Code or it didn't happen." The repositories section shows several projects, including "phenology-two-trait-migration-kint", "carnivore-local-adaptation", "qualitative-modelling", "tweak", and "tweak". The contribution graph shows activity from December 2023 to November 2024. The organizations section lists "National University of Singapore" and "Singapore Science Centre".

The screenshot shows the nadiah.org website. The header includes the name "Nadiah Pardele Kristensen" and navigation links for "About me", "Contact", and "Papers". The main content area features a grid of six images with captions: "Evolution of cooperation", "Estimating undiscovered extinctions", "Boolean approach to qualitative network modelling", "carnivore effects and local adaptation", "Ecology of Information", and "Migratory bird phenology". Below the grid is a list of hashtags: #climate\_change, #coding, #cooperation, #dispersal, #evolutionary\_ecology, #food\_web, #macroecology, #morbidity, #qualitative\_modelling, #searching, and #self\_renewed\_extinction. The page also includes a section titled "Check if an Iterated Prisoner's Dilemma strategy is a subgame perfect Nash equilibrium" and a section titled "A summary of Richard Joyce's 'The Evolution of Morality'".