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

Nadiah P. Kristensen (she/her) nadiah@nadiah.org May 2025

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 this land has always been a place of teaching, learning, and research.

Coauthors:



Ryan Chisholm National University of Singapore



Hisashi Ohtsuki The Graduate University for Advanced Studies Japan

Public goods game

- Example:
 - 1. Four individuals
 - 2. Project multiples contributions by 1.2
 - 3. Returns are split equally



- Group-game version of Prisoner's Dilemma
 - Max total payoffs if everyone contributes
 - But max individual payoff if you don't contribute
 - Marginal per-capita return = 1.2/4 = 0.3 < 1
 - i.e., 30c back per \$1 contributed
- Never makes sense to contribute

How do people really behave in linear PGGs?

- Example: Burton-Chellew et al. (2016, PNAS)
 - Elicited contributious 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!



- 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





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



Nonlinear public goods game

- Claim: sigmoid-shaped benefit functions particularly relevant to our early history
- Defectors always get higher payoffs than Cooperators



Nonlinear public goods game

- Claim: sigmoid-shaped benefit functions particularly relevant to our early history
- Defectors always get higher payoffs than Cooperators
- However, if you are in a group that's one cooperator short of the threshold, you should cooperate
- In general:
 - if cooperators rare, don't cooperate
 - if cooperators common, might get higher payoffs if you're a cooperator



Nonlinear public goods game: evolutionary perspective

- In general:
 - if cooperators rare, don't cooperate
 - if cooperators common, might get higher payoffs if you also cooperate
- Evolutionary perspective:
 - if cooperators rare (invasion), cooperation can't succeed
 - if cooperators common, cooperation might persist



Replicator dynamics approach:

- Strategies (cooperate, defect) genetically encoded
- Clonal reproduction in an infinite population
- $\bullet\,$ Higher payoff in the game $\rightarrow\,$ higher reproductive success

Change in proportion of *x*-strategists:

expected payoff to x-strategists

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

proportion of x-strategists

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

Replicator dynamics well-mixed

expected payoff to x-strategists

$$\dot{p}_{x} = p_{x} \left(\frac{\dot{\pi}_{x}}{\pi_{x}} - \sum_{i=1}^{m} p_{i} \overline{\pi}_{i} \right)$$

- 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:

$$\overline{\pi}_{C} = \sum_{g_{nf}=0}^{n-1} \pi(e_{C}, g_{nf}) \mathbb{P}[G_{nf} = g_{nf}], \text{ binomial}$$

$$= \sum_{g_{nf}=0}^{n-1} \pi(e_{C}, g_{nf}) \binom{n-1}{g_{nf}} p_{C}^{g_{nf}} (1-p_{C})^{n-1-g_{nf}}$$

Two main results about nonlinear games

Recommend: 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...



But 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: Genetic homophily was higher in the past

(ka)				
	symbolic items & transport	social care	large game	hunting technology
4000 -			first marrow extraction? [in 1]	
3000 -			marrow extraction [in 1]	first Oldowan tech
2000 .			first early carcass access? [3] widespread butchery [in 1, 6]	endurance rupping [5]
2000	raw material < 1 km [13]	toothless hominin [in 2]	possible early carcass access [4]	first Acheulean tech
				nand-axe, connonci scavenging: [7]
1000 -	raw material < 15 km [13]		regular early carcass access [4]	
1000				hafting points? [8]
				stylistically diverse points [in 13]
500			nerforated horse scanula (in 8)	
400 -		craniosinostosis child (in 2)	periorated noise scapaig (in of	first simple spear [9, 10]
300 -	ochre, obsidian >25 km [16]	neanderthal examples		hafted spears [in 11]
200 -				
200				
	first shell beads? [18]			
100 -	~200 km obsidian [in 13]			spear throwing tech? [in 11] bow and arrow [in 11]
50 -				
40 -	beads everywhere [20]			
30 -	shell beads 300-500 km [14]			large-scale fishing [12]

Replicator dynamics with homophilic group formation

expected payoff to x-strategists

$$\dot{p}_{x} = p_{x} \left(\overline{\pi}_{x} - \sum_{i=1}^{m} p_{i} \overline{\pi}_{i} \right)$$
proportion of x-strategists
$$\uparrow \text{ expected payoff in population}$$

but now expected payoff:

non

$$\bar{\pi}_{C} = \sum_{g_{nf}=0}^{n-1} \pi(e_{C}, g_{nf}) \mathbb{P}[G_{nf} = g_{nf} \mid G_{0} = e_{C}]$$
focal strategy distribution depends on focal's strategy

Colours are strategies, boxes are families:

Some notation (Hisashi's previous work)

Let ρ_ℓ be the probability that ℓ players sampled without replacement from the group have strategy 1.

prob. ℓ sampled have *m* common ancestors

$$\rho_{\ell} = \sum_{m=1}^{\ell} \begin{array}{c} & & \\ \theta_{\ell \to m} & & \\ & \uparrow \text{ propn. strategy-1 in populatn} \end{array}$$

Examples:

- Sample 1 individual: $\rho_1 = p_1$
- Sample 2 individuals:

prob. same ancestor prob. strategy-1

$$\rho_2 = \begin{array}{c} \theta_{2 \rightarrow 1} \\ p_1 + \theta_{2 \rightarrow 2} \end{array} \begin{array}{c} \rho_1^2 \\ p_1 \\ p_2 \end{array}$$
prob. two ancestors prob. both strategy-1

Ohtsuki (2014, Phil Trans R Soc):

$$\dot{\rho}_{1} = \sum_{g_{nf}=0}^{n-1} \sum_{\ell=g_{nf}}^{n-1} (-1)^{\ell-g_{nf}} \binom{\ell}{g_{nf}} \binom{n-1}{\ell}$$
relatedness terms
$$\left[(1-\rho_{1}) \rho_{\ell+1} \pi(e_{1}, g_{nf}) - \rho_{1} (\rho_{\ell} - \rho_{\ell+1} \pi(e_{2}, g_{nf})) \right]$$
payoff terms

Linear PGG is a function of dyadic relatedness only

• If the PGG is linear, only need dyadic relatedness

dyadic relatedness, Hamilton's r

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

because:

• Payoff function in *n*-player linear game can be written as a sum of payoffs in 2-player games

$$\begin{array}{c} \pi^{(n)}(e_x,g_{\mathrm{nf}}^{(n)}) \equiv \sum_{g_{\mathrm{nf}}^{(2)}} \pi^{(2)}(e_x,g_{\mathrm{nf}}^{(2)}) \\ payoff \text{ in } n\text{-player game} \end{array}$$

- So *n*-player linear game = sum of 2-player games
- · So only dyadic relatedness is needed to calculate expected payoff
- But if the payoff function is nonlinear, higher-order relatedness coefficients are needed (e.g., θ_{3→1}, θ_{3→2}, θ_{4→1}, etc.)

From group family-size distribution. For example:

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

So if we can calculate the F_q , we can calculate the needed $\theta_{l \to m}$

10

Homophilic group-formation models

Kristensen et al. (2022); Martin & Lessard

(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

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



(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).



NOTE: can be interpreted in terms of 'matching rules', i.e., strategy homophily *sensu* Jensen & Rigos (2018, Int J Game Theory)

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.









- Cooperation cannot invade a threshold game
 - Also true for sigmoid games in general (Peña et al., 2014)
- Can arise through historical homophily



- For cooperation to persist, either:
 - · Parameters such that it can be sustained in a well-mixed population
 - Some degree of homophily maintained

- 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
 - Kerr and Kaufman-Gilliland (1994, J Pers Soc Psychol)
- Commitment distinguishes us from other apes
 - In a experimental situation where one individual receives their reward early, 3.5-year-old children will continue contributing until their partner also receives their reward (Hamann et al., 2012), whereas chimpanzees don't distinguish between continuing to help in an existing collaboration versus starting a new one (Greenberg et al., 2010).



Hamann and Warneken (2012, Child Dev)

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
 - And 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

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 arepsilon

old threshold 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 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?
- New strategy: Liars



New notation

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



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

Many strategies

How does a trait change frequency over time?

dynamics of propn. of
$$s_x$$

$$\Delta p_x = \mathbb{C} \text{ov} [G_{0,x}, W_0],$$
focal's strategy indicator fitness of focal

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



George Robert Price

(... some useful covariance identities ...)



Other member accounting



Payoff to the focal individual:

$$\Pi_{0} = \sum_{i=1}^{m} \begin{array}{c} G_{0,i} \\ \hline & \\ \end{array} \begin{pmatrix} \mathbf{e}_{i}, \ \mathbf{G}_{nf} \\ \hline & \\ \end{array} \end{pmatrix}$$
 nonfocal strategy composition

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

$$\Delta p_{x} = \mathbb{E} \left[G_{0,x} \ \pi(\boldsymbol{e}_{x}, \boldsymbol{G}_{\mathrm{nf}}) \right] - p_{x} \sum_{i=1}^{m} \mathbb{E} \left[G_{0,i} \ \pi(\boldsymbol{e}_{i}, \boldsymbol{G}_{\mathrm{nf}}) \right]$$

Other member accounting

nonfocal strategy composition

$$\Delta p_{x} = \mathbb{E}\left[G_{0,x} \ \pi(\boldsymbol{e}_{x}, \ \boldsymbol{G}_{\mathrm{nf}})\right] - p_{x} \sum_{i=1}^{m} \mathbb{E}\left[G_{0,i} \ \pi(\boldsymbol{e}_{i}, \ \boldsymbol{G}_{\mathrm{nf}})\right]$$

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

$$\mathbb{E}\left[G_{0,i}\pi(\boldsymbol{e}_{i},\boldsymbol{G}_{\mathrm{nf}})\right] = \sum_{\boldsymbol{g}_{\mathrm{nf}}\in\mathcal{G}_{\mathrm{nf}}} \pi(\boldsymbol{e}_{i},\boldsymbol{g}_{\mathrm{nf}}) \mathbb{P}[\boldsymbol{G}_{0} = \boldsymbol{e}_{i},\boldsymbol{G}_{\mathrm{nf}} = \boldsymbol{g}_{\mathrm{nf}}\right]$$
$$= \sum_{\boldsymbol{g}_{\mathrm{nf}}\in\mathcal{G}_{\mathrm{nf}}} \pi(\boldsymbol{e}_{i},\boldsymbol{g}_{\mathrm{nf}}) \underbrace{\mathbb{P}[\boldsymbol{G}_{0} = \boldsymbol{e}_{i}]}_{p_{i}} \mathbb{P}[\boldsymbol{G}_{\mathrm{nf}} = \boldsymbol{g}_{\mathrm{nf}} \mid \boldsymbol{G}_{0} = \boldsymbol{e}_{i}]$$
$$= p_{i} \underbrace{\sum_{\boldsymbol{g}_{\mathrm{nf}}\in\mathcal{G}_{\mathrm{nf}}} \pi(\boldsymbol{e}_{i},\boldsymbol{g}_{\mathrm{nf}})}_{\overline{\pi}_{i}} \mathbb{P}[\boldsymbol{G}_{\mathrm{nf}} = \boldsymbol{g}_{\mathrm{nf}} \mid \boldsymbol{G}_{0} = \boldsymbol{e}_{i}]}_{\overline{\pi}_{i}}$$

Recovered replicator eqn: $\Delta p_x \propto p_x \left(\overline{\pi}_x - \sum_{i=1}^m p_i \overline{\pi}_i\right) = p_x \left(\overline{\pi}_x - \overline{\pi}\right).$ But $\mathbb{P}[\boldsymbol{G}_{nf} = \boldsymbol{g}_{nf} \mid \boldsymbol{G}_0 = \boldsymbol{e}_i]$ is not obvious: $\bullet \bullet \bullet \bullet$

Whole-group accounting

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



This time, focus on the whole-group distribution. new payoff fnc wrt whole-group strategy composition

$$\Pi_0 = \sum_{i=1}^m G_{0,i} \left[\hat{\pi}(\boldsymbol{e}_i, \boldsymbol{G}_{\mathrm{a}}) \right]$$

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

$$\Delta p_{x} = \sum_{\boldsymbol{g}_{a} \in \mathcal{G}_{a}} \left(\frac{g_{a,x}}{n} \hat{\pi}(\boldsymbol{e}_{x}, \boldsymbol{g}_{a}) - p_{x} \sum_{i=1}^{m} \frac{g_{a,i}}{n} \hat{\pi}(\boldsymbol{e}_{i}, \boldsymbol{g}_{a}) \right) \mathbb{P}[\boldsymbol{G}_{a} = \boldsymbol{g}_{a}]$$
prob. of whole-group strategy composition











$$\mathbb{P}[\boldsymbol{G}_a = oldsymbol{\square} \boldsymbol{\mathcal{P}}[\boldsymbol{G}_a = oldsymbol{\square} \boldsymbol{\mathcal{P}}[\boldsymbol{Z} = oldsymbol{z}]$$
 $= \sum_{oldsymbol{z} \in \mathcal{Z}_{oldsymbol{g}_a}} \mathbb{P}[oldsymbol{Z} = oldsymbol{z}]$







Probability of strategywise family-size distribution:

get from homophilic group-formation model

$$\mathbb{P}[\boldsymbol{G}_{a} = \boldsymbol{g}_{a}] = \sum_{\boldsymbol{z} \in \mathcal{Z}_{\boldsymbol{g}_{a}}} F_{\boldsymbol{y}} C(\boldsymbol{z}) A(\boldsymbol{z}, \boldsymbol{p})$$
count of multiset permutations
nbr. families pursuing strategy s_{i}

$$A(\boldsymbol{z}, \boldsymbol{p}) = \prod_{i=1}^{m} p_{i}^{||\boldsymbol{z}_{i}||}$$

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

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

18

Bringing it all together:

prob. focal pursues
$$S_x$$

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

- Not as intuitive as the traditional replicator equation
 - $\Delta p_{\scriptscriptstyle X} \propto p_{\scriptscriptstyle X} \left(\overline{\pi}_{\scriptscriptstyle X} \overline{\pi}
 ight)$
- Might be useful from computational perspective because we've split homophily calculations off from strategy identity
- Now it's clearer how to calculate $\mathbb{P}[\boldsymbol{G}_{\mathrm{nf}} = \boldsymbol{g}_{\mathrm{nf}} \mid \boldsymbol{G}_{0} = \boldsymbol{e}_{i}]$

Aside: Payoff-matrix transformation example (2 players)

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

$$\overline{\boldsymbol{\pi}} = \begin{pmatrix} \overline{\pi}_1 \\ \vdots \\ \overline{\pi}_m \end{pmatrix} = \begin{pmatrix} \frac{\mathbf{i}_{g}}{\mathbf{i}_{g}} \\ \vdots \\ \mathbf{a}_{m,1} \\ \mathbf{a}_{m,1} \\ \mathbf{a}_{m,1} \\ \mathbf{a}_{m,1} \\ \mathbf{a}_{m,1} \\ \mathbf{a}_{m,m} \end{pmatrix} \begin{pmatrix} p_1 \\ \vdots \\ p_m \end{pmatrix} = \begin{pmatrix} a_{1,1}p_1 + \ldots + a_{1,m}p_m \\ \vdots \\ a_{m,1}p_1 + \ldots + a_{m,m}p_m \end{pmatrix}$$

• Now with homophily, dyadic relatedness $heta_{2
ightarrow 1}$

$$B = \theta_{2 \to 1} \begin{pmatrix} a_{1,1} & \dots & a_{1,1} \\ \vdots & & \vdots \\ a_{m,m} & \dots & a_{m,m} \end{pmatrix} + (1 - \theta_{2 \to 1}) \begin{pmatrix} a_{1,1} & \dots & a_{1,m} \\ \vdots & & \vdots \\ a_{m,1} & \dots & a_{m,m} \end{pmatrix}$$

i matched with *i* with prob. $\theta_{2 \to 1}$ *i* matched with random with prob. $1 - \theta_{2 \to 1}$

• Dynamics of A with homophily \equiv dynamics of B well-mixed $\dot{p}_i = p_i((\begin{array}{c} B \end{array} \boldsymbol{p})_i - \boldsymbol{p}^T \begin{array}{c} B \end{array} \boldsymbol{p})$ Seeking a solution to:



Aside: Payoff transformation *n* players



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)

Coordinated cooperation

- Game with 4 strategies:
 - 1. D: unconditional Defector, never contributes
 - 2. C: Coordinating cooperator, hold lottery, follow through if chosen
 - Nbr. contributors $\tau={\rm threshold},$ 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 ε 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







































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





of evaluationary processes rather than tracking moral traffic. While evolution has equipped us with the capacity for moral judgement, this doesn't necessarily mean that our moral beliefs are true or justified, instead, our moral sense evolved because it was useful for our