https://doi.org/10.1038/s41586-019-1488-5

Social dilemmas among unequals

Oliver P. Hauser[1,6]*, Christian Hilbe[2,6]*, Krishnendu Chatterjee[2] & Martin A. Nowak[3,4,5]*

Direct reciprocity is a powerful mechanism for the evolution of cooperation on the basis of repeated interactions[1–4]. It requires that interacting individuals are sufficiently equal, such that everyone faces similar consequences when they cooperate or defect. Yet inequality is ubiquitous among humans[5,6] and is generally considered to undermine cooperation and welfare[7–10]. Most previous models of reciprocity do not include inequality[11–15]. These models assume that individuals are the same in all relevant aspects. Here we introduce a general framework to study direct reciprocity among unequal individuals. Our model allows for multiple sources of inequality. Subjects can differ in their endowments, their productivities and in how much they benefit from public goods. We find that extreme inequality prevents cooperation. But if subjects differ in productivity, some endowment inequality can be necessary for cooperation to prevail. Our mathematical predictions are supported by a behavioural experiment in which we vary the endowments and productivities of the subjects. We observe that overall welfare is maximized when the two sources of heterogeneity are aligned, such that more productive individuals receive higher endowments. By contrast, when endowments and productivities are misaligned, cooperation quickly breaks down. Our findings have implications for policy-makers concerned with equity, efficiency and the provisioning of public goods.

In social dilemmas, overall welfare is maximized if all individuals cooperate yet each individual prefers to defect[16]. Such dilemmas occur at all levels of human society. They affect families, companies and nations[17,18]. An extensive body of research has shown that cooperation is more likely when groups are stable and subjects interact repeatedly[11–15]. However, this mechanism of direct reciprocity assumes that group members have sufficient leverage to influence one another. Subjects need to be able to give appropriate responses. Tit-for-tat can only be effective if it incentivizes others to cooperate. Most previous models of reciprocity assume perfect symmetry between individuals[11–15]. Real groups often exhibit substantial heterogeneity, which is derived from multiple sources[5,6]. Experimental studies have shown that inequality in the endowments of the players reduces cooperation[7,8] and undermines the social structure of a population[9]. Even if subjects start out equally, game dynamics can introduce inequality over time, disfavouring individuals who are more cooperative[19] (Supplementary Information). So far, it has been difficult to predict the effect of heterogeneity on cooperation, especially if subjects vary along multiple dimensions. Here we propose a general framework to explore how different kinds of heterogeneities interact and affect cooperation.

We consider public goods games with n players. In each round, player i receives a fixed endowment e_i, which can be interpreted as a regular income. After receiving their endowments, players independently decide which fraction x_i of their endowment to contribute to the public good. The payoff u_i of player i for that round depends on the distribution of endowments, $e_1, \ldots, e_n$, and on the relative contributions of the players, $x_1, \ldots, x_n$. It is typically assumed that all players have the same endowment and that contributions to the public goods are multiplied by a common productivity factor, r (Fig. 1a). Here we instead consider interactions in which players have different endowments, different productivities or for which payoffs are nonlinear (Fig. 1b–d).

As a specific example, we consider public goods games in which the contributions of each player are multiplied by an individual factor r_i and equally shared among all participants,

$$u_i = \frac{1}{n}\sum_{j=1}^{n} r_j e_j x_j + (1-x_i)e_i \quad (1)$$

The first term represents the payoff that is derived from the public good and the second term represents the remaining endowment of the player. We interpret the factors r_j as the productivity of each player and assume $1 < r_j < n$ for all j. Thus, the game is a social dilemma in which individuals have an incentive to free-ride[16]. Although we focus on the example given by equation (1) throughout most of the main text, our findings generalize to arbitrary public goods games that satisfy four natural requirements (Methods).

If the public goods game is played once, defection is the only equilibrium. But for repeated interactions, cooperation can prevail if players adopt conditional strategies, such as tit-for-tat[2] or win-stay lose-shift (WSLS)[11], or multiplayer variants of these strategies[20]. We assume after each round that there is another round with probability δ.

To explore the effects of different kinds of heterogeneity, we first characterize when it is that cooperation can be maintained. For a

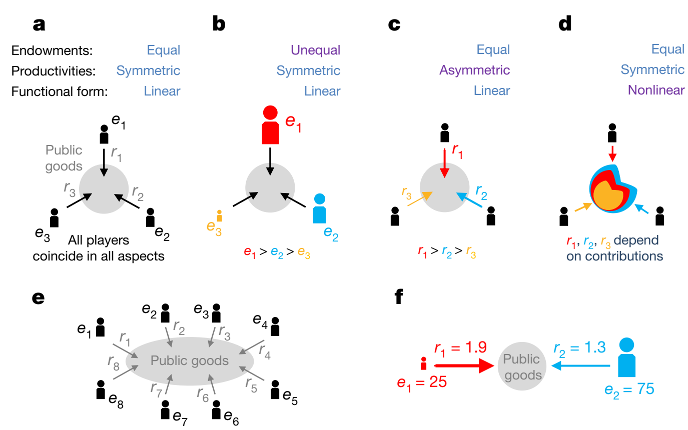


Fig. 1 | Public goods games among unequals. We consider social dilemmas in which participants decide how much of their endowment e_i to contribute to the public goods. The contributions of each player are multiplied by r_i and then divided among all players. The players have equal endowments if $e_1 = e_2 = e_3$. The game is symmetric if players are indistinguishable except for their endowments and contributions. Here the game is symmetric if $r_1 = r_2 = r_3$. The game is linear if the payoffs depend linearly on the endowments and contributions of the players. Here the game is linear if the factors r_i are constant. **a**, Most previous studies assume that players have the same endowment, the game is symmetric and payoffs are linear. **b**–**d**, Instead, we allow players to have different endowments, different productivities and nonlinear payoffs. **e**, We derive general results for n-player games. **f**, As a special case, we study pairwise interactions.

[1]Department of Economics, University of Exeter Business School, Exeter, UK. [2]IST Austria, Klosterneuburg, Austria. [3]Program for Evolutionary Dynamics, Harvard University, Cambridge, MA, USA. [4]Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, USA. [5]Department of Mathematics, Harvard University, Cambridge, MA, USA. [6]These authors contributed equally: Oliver P. Hauser, Christian Hilbe. *e-mail: o.hauser@exeter.ac.uk; christian.hilbe@ist.ac.at; martin_nowak@harvard.edu

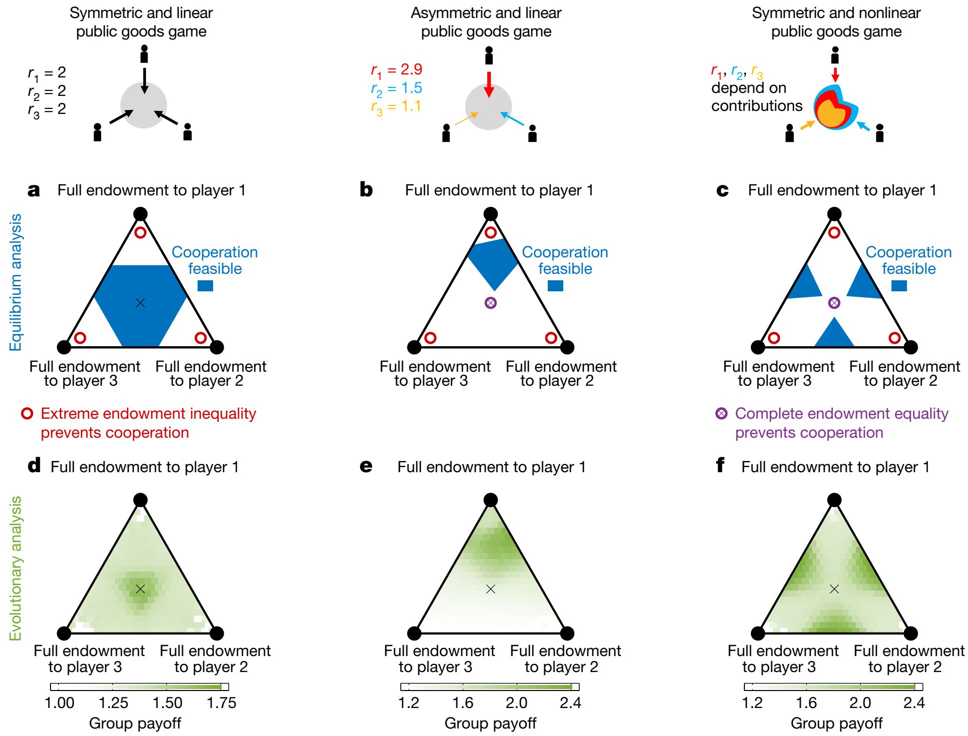


Fig. 2 | Feasibility and evolvability of cooperation in public goods games among unequals. a–f, We consider groups of three players who interact in three different public goods games. In each case, we investigated when equal endowments help to maintain cooperation (**a**–**c**) or favour its evolution (**d**–**f**). The triangles represent the possible ways to distribute the initial endowment among the players. Corners correspond to distributions for which one player receives all of the endowment. Edges correspond to distributions for which one player receives no endowment. The centre of the triangle marks equal endowments. 'Group payoff' corresponds to the total payoff across all group members, averaged over 10^6 time steps of an evolutionary simulation. We find that extreme inequality is always detrimental to cooperation. However, when the game is asymmetric or nonlinear, slightly unequal endowments may be necessary for cooperation to be feasible (**b**, **c**) and for cooperation to evolve (**e**, **f**).

given public goods game and a given endowment distribution, we say that full cooperation is feasible if there is a subgame perfect equilibrium in which all players always contribute their entire endowment. In such an equilibrium, players have no incentive to deviate after any history of previous play[21]. In the Supplementary Information, we prove that cooperation is feasible if and only if the strategy Grim is an equilibrium. Grim cooperates unless another player has defected in a previous round[3]. From the equilibrium condition for Grim, it follows that cooperation is feasible for the public good game given by equation (1) if and only if for all players i with $e_i > 0$ the following condition holds:

$$\frac{\delta}{n}\sum_{j\neq i} r_j e_j \geq \left(1-\frac{r_i}{n}\right)e_i \qquad (2)$$

The expected benefit from the future cooperation of others must exceed the incentive to defect in the present round. For cooperation to be feasible, future losses must outweigh present gains.

On the basis of this general characterization of when cooperation is feasible, we derive a number of results. First, cooperation is never feasible if there is too much inequality, such that most of the endowment is in the hands of one player (Supplementary Information). For linear and symmetric games (Fig. 1), we show that if cooperation is feasible at all, it is feasible for equal endowments (Fig. 2a). However, if the game is asymmetric (Fig. 2b) or nonlinear (Fig. 2c), full cooperation may only be feasible when players have unequal endowments. In such a case it can even be optimal to give some players no initial endowment at all.

To gain intuition, consider a case in which players differ in productivities, $r_1 > \ldots > r_n$. We find a twofold advantage of giving higher endowments to more productive players. First, there is a stability advantage: an unequal distribution of endowments makes it easier for full cooperation to be an equilibrium. To understand this, assume instead that players receive equal endowments. Then inequality (2) suggests that cooperation is feasible if

$$\delta \geq \frac{n-r_n}{R-r_n} \qquad (3)$$

in which $R = r_1 + \ldots + r_n$ is the sum of all productivities. For equal endowments, player n with the lowest productivity faces the largest temptation to defect, because this player has the highest marginal cost $1 - r_n/n$ of contributing. This temptation can be counterbalanced by allocating a smaller endowment to player n who then has less to gain from withholding, whereas the others have more leverage to retaliate in future rounds. Both effects enhance the stability of cooperation. Second, there is an efficiency advantage of unequal endowments. Because contributions of more productive players are multiplied by a higher factor, social welfare is maximized when the most productive player obtains the largest share of the initial endowment—subject to the constraint that full cooperation is feasible.

If the game involves only two players, we can compute which endowment distribution is the most conducive to cooperation. An endowment distribution is maximally cooperative if it requires the lowest continuation probability δ for cooperation to be feasible. Using inequality (2), we show in the Supplementary Information that endowments need to be distributed as

$$\frac{e_1}{e_2} = \sqrt{\frac{r_2(2-r_2)}{r_1(2-r_1)}} \qquad (4)$$

An equal distribution, $e_1 = e_2$, is maximally cooperative only if players have the same productivities. Otherwise, the more productive player should have a larger share of the endowment.

After exploring under which conditions cooperation is feasible, we study when it is that cooperation can evolve[3]. To make an evolutionary

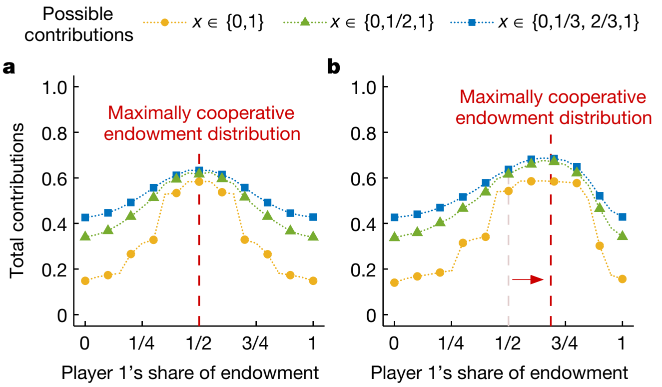


Fig. 3 | When players differ in their productivities, equal endowments do not maximize contributions. We consider public goods games between two players. **a**, **b**, Players either coincide in their productivities, $r_1 = r_2 = 1.6$ (**a**) or player 1 is more productive, $r_1 = 1.9$ and $r_2 = 1.3$ (**b**). In each case, we vary player 1's share of the initial endowment. We perform evolutionary simulations (dotted lines) for three scenarios, depending on which fraction of the endowment the players can contribute: {0, 1}, {0, 1/2, 1} or {0, 1/3, 2/3, 1}. For equal productivities, cooperation is most likely to emerge when both players receive the same endowment. By contrast, when players differ in productivity, the maximum total payoff is achieved when player 1 obtains a larger fraction of the endowment. The position of the maximum is well-approximated by the maximally cooperative endowment distribution given by equation (4).

approach computationally tractable, we first consider players who respond only to the outcome of the last round. Moreover, we assume that players choose only from a finite set of possible contributions. For example, they may either contribute their full endowment or nothing at all. In that case, we refer to the two possible actions as cooperation and defection, respectively. With some small probability, ε, players commit errors such that a player who intends to cooperate defects by mistake (and vice versa). Players adopt new strategies over time by comparing their payoff to the payoff they would obtain by using a random alternative strategy. The better the payoff of the alternative strategy, the more likely players are to switch. We iterate this process for many steps and record the average cooperation rates over time (Methods).

Our numerical findings parallel the previous equilibrium results. Cooperation cannot evolve if one of the players receives almost all of the endowment. Moreover, for linear and symmetric games, individuals are most likely to cooperate if everyone receives the same endowment (Fig. 2d). However, if some players are more productive than others (Fig. 2e) or if the game is nonlinear (Fig. 2f), unequal endowments yield more cooperation and higher payoffs. In all cases, we observe that the strategy Grim is less relevant, because it cannot sustain cooperation in the presence of noise[3]. Instead, cooperation evolves if the strategy WSLS[11] is an equilibrium (Extended Data Figs. 1–5). WSLS contributes the full endowment in the first round, or if all players made the same relative contribution in the previous round. Otherwise WSLS contributes nothing[11,20].

In the simulations, a group of defectors is most likely to be invaded by strategies such as tit-for-tat. These conditional cooperators in turn quickly adopt WSLS, which is more robust with respect to errors. However, because of stochasticity, any strategy is replaced eventually, even if it is an equilibrium (Supplementary Information). Further simulations show that analogous results hold when players choose between more than two discrete contributions each round (Fig. 3) or when strategies are represented by finite-state automata[15] (Extended Data Fig. 6, see Supplementary Information for details).

To explore the applicability of these theoretical results, we designed an online behavioural experiment based on the two-player game of Fig. 3. Participants are either equally productive or not and have the same endowment or not. We consider five treatments: full equality, endowment inequality, productivity inequality, aligned inequality and

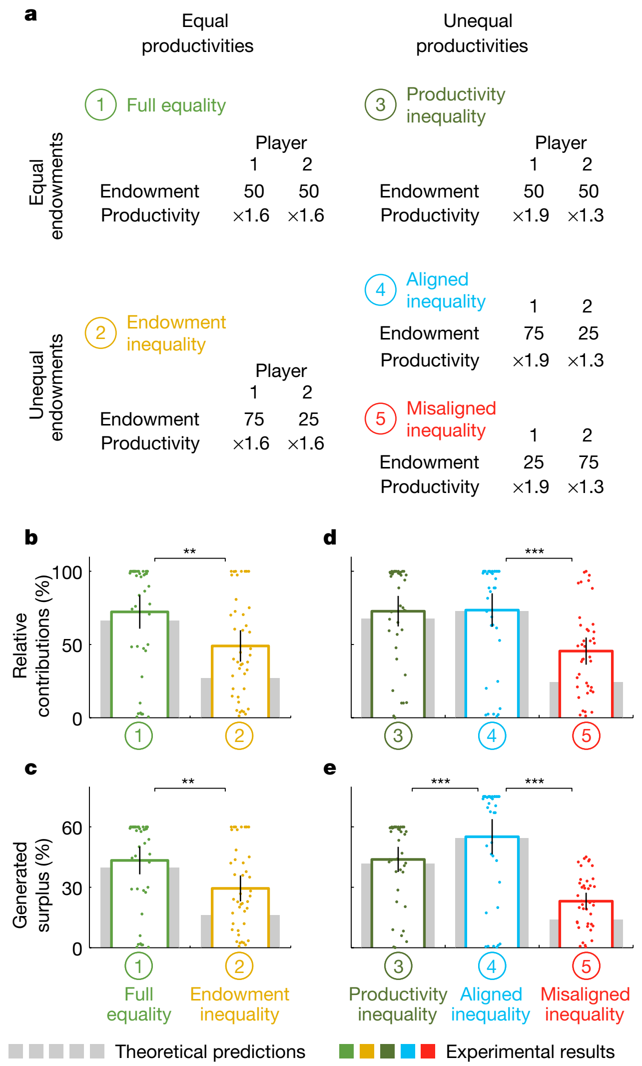


Fig. 4 | Exploring the effects of multidimensional inequality with a behavioural experiment. a, On the basis of the two-player game shown in Fig. 3, we conduct an experiment with varying endowments and productivities. There are five conditions: (1) full equality, (2) endowment inequality, (3) productivity inequality, (4) aligned inequality (the more productive player has higher endowment), and (5) misaligned inequality (the more productive player has lower endowment). **b–e**, For each treatment, we compare the theoretical predictions from evolutionary simulations (grey bars) with the respective average values of the experiment (coloured bars). We show the relative contributions of each player (top) and the generated surplus (by how much the total payoffs of the players exceed their initial endowments; bottom). Aligned inequality yields high cooperation rates and higher payoffs than other treatments. Coloured dots represent individual groups of players; the number of observations (groups) for each treatment was 42, 42, 40, 39, 40 for treatments 1–5, respectively. Error bars represent 95% confidence intervals. We analysed pairwise differences between treatments using two-tailed Mann–Whitney U-tests. $^{**}P < 0.01$; $^{***}P < 0.001$. See Methods for details.

misaligned inequality (Fig. 4a). In the last two treatments, individuals differ in both dimensions. Either the more productive player (aligned) or the less productive player (misaligned) receives the larger endowment. Previous experiments suggest that—in isolation—heterogeneous endowments reduce cooperation[7,8], whereas heterogeneous productivities have a negligible effect[22]. Here we study the interaction between the two heterogeneities in repeated games, for which previous research did not find any significant effects[23].

On the basis of our evolutionary analysis, we expect aligned inequality to increase and misaligned inequality to reduce welfare compared to the case of productivity inequality alone (Fig. 3). The experiment confirms these predictions (Fig. 4b–e). Aligned inequality results in substantially higher contributions than misaligned inequality and generates the highest surplus across all treatments. Under aligned inequality, most high-endowment players match the relative contribution of the low-endowment players. That is, if the low-endowment player gives their full endowment, then so does the high-endowment player, even if their absolute contributions are three times higher. By contrast, contributions under misaligned inequality do not follow a clear norm; often, the high-endowment player only matches the absolute contribution of the other player (Extended Data Figs. 7–10 and Supplementary Information).

Here we introduce a general framework to study direct reciprocity among unequals. Our three complementary approaches—equilibrium calculations, evolutionary simulations and a behavioural experiment—suggest an unexpected benefit of inequality. We show that equal endowments can be detrimental to social welfare if subjects differ along multiple other dimensions, such as productivity or benefits from public goods. In those cases, some inequality can increase both the stability of cooperation and the efficiency of contributions.

Despite these potential benefits, inequality comes with caveats. First, maximizing cooperation requires a delicate balance between the different dimensions of heterogeneity. Finding the right amount of inequality can prove difficult when the players' personal characteristics, such as their productivities, are known only imperfectly. The problem is aggravated by our finding that an excess of inequality is always detrimental.

Second, endowment inequality could interfere with institutional solutions to cooperation. For example, when cooperation is maintained through sanctions, heterogeneous groups may disagree on which norm to enforce[24]. Additional problems arise when sanctioning institutions can be corrupted[25,26], especially when better-endowed individuals can 'play the system'.

Finally, reducing inequality is often considered an important policy objective in itself. Humans dislike inequality[27] and are sometimes willing to sacrifice their own wealth to guarantee more-egalitarian outcomes[28,29]. In addition, inequality often renders successful coordination in social dilemmas difficult, as different actors may disagree on which cooperative equilibrium is fair[30]. However, here we show that inequality does not need to render cooperation impossible. When individuals are naturally heterogeneous, moderate inequality can be necessary for cooperation to prevail.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-019-1488-5.

Received: 20 November 2018; Accepted: 11 July 2019;
Published online: 14 August 2019

1. Trivers, R. L. The evolution of reciprocal altruism. *Q. Rev. Biol*. **46**, 35–57 (1971).
2. Axelrod, R. *The Evolution of Cooperation* (Basic Books, 1984).
3. Sigmund, K. *The Calculus of Selfishness* (Princeton Univ. Press, 2010).
4. Nowak, M. A. Five rules for the evolution of cooperation. *Science* **314**, 1560–1563 (2006).
5. Piketty, T. & Saez, E. Inequality in the long run. *Science* **344**, 838–843 (2014).
6. Scheffer, M., van Bavel, B., van de Leemput, I. A. & van Nes, E. H. Inequality in nature and society. *Proc. Natl Acad. Sci. USA* **114**, 13154–13157 (2017).
7. Cherry, T. L., Kroll, S. & Shogren, J. F. The impact of endowment heterogeneity and origin on public good contributions: evidence from the lab. *J. Econ. Behav. Organ*. **57**, 357–365 (2005).
8. Hargreaves Heap, S. P., Ramalingam, A. & Stoddard, B. Endowment inequality in public good games: a re-examination. *Econ. Lett.* **146**, 4–7 (2016).
9. Nishi, A., Shirado, H., Rand, D. G. & Christakis, N. A. Inequality and visibility of wealth in experimental social networks. *Nature* **526**, 426–429 (2015).
10. Hauser, O. P., Kraft-Todd, G. T., Rand, D. G., Nowak, M. A. & Norton, M. I. Invisible inequality leads to punishing the poor and rewarding the rich. *Behav. Public Policy* https://doi.org/10.1017/bpp.2019.4 (2019).
11. Nowak, M. & Sigmund, K. A strategy of win-stay, lose-shift that outperforms tit-for-tat in the Prisoner's Dilemma game. *Nature* **364**, 56–58 (1993).
12. Szabó, G., Antal, T., Szabó, P. & Droz, M. Spatial evolutionary prisoner's dilemma game with three strategies and external constraints. *Phys. Rev. E* **62**, 1095–1103 (2000).
13. Doebeli, M. & Hauert, C. Models of cooperation based on the prisoner's dilemma and the snowdrift game. *Ecol. Lett.* **8**, 748–766 (2005).
14. Stewart, A. J. & Plotkin, J. B. From extortion to generosity, evolution in the Iterated Prisoner's Dilemma. *Proc. Natl Acad. Sci. USA* **110**, 15348–15353 (2013).
15. van Veelen, M., García, J., Rand, D. G. & Nowak, M. A. Direct reciprocity in structured populations. *Proc. Natl Acad. Sci. USA* **109**, 9929–9934 (2012).
16. Kerr, B., Godfrey-Smith, P. & Feldman, M. W. What is altruism? *Trends Ecol. Evol*. **19**, 135–140 (2004).
17. Rand, D. G. & Nowak, M. A. Human cooperation. *Trends Cogn. Sci*. **17**, 413–425 (2013).
18. Frank, M. R. et al. Detecting reciprocity at a global scale. *Sci. Adv*. **4**, eaao5348 (2018).
19. Gächter, S., Mengel, F., Tsakas, E. & Vostroknutov, A. Growth and inequality in public good provision. *J. Public Econ*. **150**, 1–13 (2017).
20. Pinheiro, F. L., Vasconcelos, V. V., Santos, F. C. & Pacheco, J. M. Evolution of all-or-none strategies in repeated public goods dilemmas. *PLOS Comput. Biol*. **10**, e1003945 (2014).
21. Fudenberg, D. & Tirole, J. *Game Theory* 6th edn (MIT Press, 1998).
22. Fisher, J., Isaac, R. M., Schatzberg, J. W. & Walker, J. M. Heterogenous demand for public goods: behavior in the voluntary contributions mechanism. *Public Choice* **85**, 249–266 (1995).
23. van Gerwen, N., Buskens, V. & van der Lippe, T. Individual training and employees' cooperative behavior: evidence from a contextualized laboratory experiment. *Rationality Soc*. **30**, 432–462 (2018).
24. Reuben, E. & Riedl, A. Enforcement of contribution norms in public good games with heterogeneous populations. *Games Econ. Behav*. **77**, 122–137 (2013).
25. Abdallah, S. et al. Corruption drives the emergence of civil society. *J. R. Soc. Interface* **11**, 20131044 (2014).
26. Muthukrishna, M., Francois, P., Pourahmadi, S. & Henrich, J. Corrupting cooperation and how anti-corruption strategies may backfire. *Nat. Hum. Behav*. **1**, 0138 (2017).
27. Tricomi, E., Rangel, A., Camerer, C. F. & O'Doherty, J. P. Neural evidence for inequality-averse social preferences. *Nature* **463**, 1089–1091 (2010).
28. Dawes, C. T., Fowler, J. H., Johnson, T., McElreath, R. & Smirnov, O. Egalitarian motives in humans. *Nature* **446**, 794–796 (2007).
29. Durante, R., Putterman, L. & Van der Weele, J. Preferences for redistribution and perception of fairness: an experimental study. *J. Eur. Econ. Assoc*. **12**, 1059–1086 (2014).
30. Tavoni, A., Dannenberg, A., Kallis, G. & Löschel, A. Inequality, communication, and the avoidance of disastrous climate change in a public goods game. *Proc. Natl Acad. Sci. USA* **108**, 11825–11829 (2011).

METHODS

General modelling framework. In the main text, we used the public goods game in equation (1) to illustrate our main findings. However, the framework that we use to study reciprocity in asymmetric social dilemmas is general and can encompass many other examples (as indicated in Fig. 2c, f). Here we introduce, in brief, our general framework. A full account is provided in the Supplementary Information.

We consider games with n players. The endowments of the players in each round are given by the endowment vector $\boldsymbol{e} = (e_1, \ldots, e_n)$. Endowments are non-negative, $e_i \geq 0$ for all players i, and normalized, $e_1 + \ldots + e_n = 1$. Given their endowments, players decide which fraction of their endowment they contribute, as summarized by the contribution vector $\boldsymbol{x} = (x_1, \ldots, x_n)$ for which $x_i \in [0, 1]$ for all players i. We refer to x_i as the relative contribution of the player and to $e_i x_i$ as the absolute contribution of the player. We use the shorthand notation $\boldsymbol{x} = \boldsymbol{0}$ if no player contributes to the public goods and $\boldsymbol{x} = \boldsymbol{1}$ if all players contribute their full endowment. Given the endowments $\boldsymbol{e}$ and the relative contributions $\boldsymbol{x}$ in a given round, the payoff for player i in that round is $u_i(\boldsymbol{e}, \boldsymbol{x})$. If there are no contributions, players receive their initial endowment $u_i(\boldsymbol{e}, \boldsymbol{0}) = e_i$.

We consider public goods games that satisfy the following four conditions: continuity (C), the payoff functions $u_i(\boldsymbol{e}, \boldsymbol{x})$ are continuous in both arguments; positive externalities (PE), as a player with a positive endowment increases their contribution, the payoffs of all other players increase; incentive to free-ride (IF), as a player with positive endowment increases their contribution, their own payoff decreases; and optimality of cooperation (OC), as a player with positive endowment increases their contribution, the overall payoff over all members of the group increases.

The first condition of continuity is merely a technical assumption that is useful for some of the analytical results. The other three conditions generalize previous notions of social dilemmas in one-shot games in which players can either cooperate or defect[16].

We note that the above conditions rule out certain threshold public goods games, in which payoffs increase discontinuously once total contributions exceed a certain threshold[31–34]. In such threshold public goods games, cooperation can often emerge even if the game is played only once, because players have an incentive not to fall below the threshold[35]. By considering public goods games that satisfy (C), (PE), (IF) and (OC), we consider the most stringent case of a social dilemma, in which repeated interactions are key to sustain positive contributions. Asymmetric threshold public goods games in a one-shot or finite-horizon setting have previously been studied[36–39]. Previous work has also explored the consequences of heterogeneities in the background fitness of the players[40], as well as strategies to maintain cooperation in the asymmetric prisoner's dilemma[41].

We can classify public goods games according to two properties, linearity and symmetry. We say a public goods game is linear if payoffs $u_i(\boldsymbol{e}, \boldsymbol{x})$ are linear in both arguments, $\boldsymbol{e}$ and $\boldsymbol{x}$. A public goods game is symmetric if players are indistinguishable, except for their endowments and for their contributions. Formally, if $\sigma = (\sigma_1, \ldots, \sigma_n)$ is a permutation of the numbers $1, \ldots, n$ and if $\boldsymbol{e}_\sigma$ and $\boldsymbol{x}_\sigma$ are the permuted endowment and contribution vectors, respectively, then the public goods game is symmetric if $u_i(\mathbf{e}, \mathbf{x}) = u_{\sigma_i}(\mathbf{e}_\sigma, \mathbf{x}_\sigma)$ for all permutations σ, endowments $\boldsymbol{e}$ and contributions $\boldsymbol{x}$. That is, if players were to switch roles with respect to their endowments and contributions, their payoffs would change accordingly. In particular, the public goods game in equation (1) is symmetric only if all players have the same productivity, $r_1 = \ldots = r_n$.

Equilibrium analysis. We explore under which conditions full cooperation can be sustained if the public goods game is repeated. After each round, there is another round with probability δ. Strategies for the repeated game are rules that tell the player which fraction of the endowment to contribute, depending on the players' endowments and on all previous contributions. If the contribution vector in round t is $\boldsymbol{x}(t)$, payoffs are given by the weighted average payoff per round, $\pi_i = (1-\delta)\sum_{t=0}^{\infty} \delta^t u_i(\mathbf{e}, \mathbf{x}(t))$.

For a given public goods game with payoff function $u = (u_1, \ldots, u_n)$, continuation probability δ and endowment distribution $\boldsymbol{e}$, we say full cooperation is feasible if there is a subgame perfect equilibrium in which all players contribute their full endowment in every round. In a subgame perfect equilibrium, no player has an incentive to deviate after any given history[21]. It is a refinement of the Nash equilibrium concept: every subgame perfect equilibrium is a Nash equilibrium, but the converse does not need to be true.

We refer to the set of all endowments for which full cooperation is feasible as $E_u(\delta)$. In Fig. 2a–c, these sets are illustrated as blue areas within the space of all endowment distributions. In the Supplementary Information, we characterize these sets for all games that satisfy the four conditions (C), (PE), (IF) and (OC). We show that the following are equivalent (Supplementary Information, proposition 1): (i) cooperation is feasible for a given endowment distribution $\boldsymbol{e}$; (ii) the condition $\delta(u_i(\boldsymbol{e}, \boldsymbol{1}_{-i}) - u_i(\boldsymbol{e}, \boldsymbol{0})) \geq u_i(\mathbf{e}, \mathbf{1}_{-i}) - u_i(\mathbf{e}, \mathbf{1})$ holds for all players i with positive endowment. Here, $\boldsymbol{1}_{-i}$ is the shorthand notation for a group in which everyone contributes the full endowment, except for player i who contributes nothing; and (iii) Grim is a subgame perfect equilibrium for the endowment distribution $\boldsymbol{e}$.

On the basis of this general characterization, we prove the following implications. First, for any given payoff function u and continuation probability δ, there is a threshold $e_i^* < 1$ such that $\boldsymbol{e} \notin E_u(\delta)$ holds for any endowment distribution $\boldsymbol{e}$ with $e_i > e_i^*$. That is, cooperation is never feasible if one of the players receives an excessive share of the endowment.

Second, if the public goods game is symmetric and linear, and $E_u(\delta) \neq \varnothing$, then $(1/n, \ldots, 1/n) \in E_u(\delta)$. That is, if full cooperation is feasible in a linear and symmetric public goods game, then it is always feasible when all players receive the same endowment.

Third, if the public goods game is either asymmetric or nonlinear, there are cases for which $E_u(\delta) \neq \varnothing$, but $(1/n, \ldots, 1/n) \notin E_u(\delta)$. That is, in asymmetric or nonlinear public goods games, full cooperation may be feasible only for unequal endowment distributions.

Evolutionary analysis. We also explored the dynamics that arises if players have not yet settled on a particular equilibrium. Instead, they may begin with randomly initialized strategies, and then learn to use more profitable strategies over time.

To this end, we first consider a simplified strategy space. We assume that the contributions of the players in any given round depend only on the outcome of the previous round, as in most previous work on evolution of reciprocity[41–63]. In addition, we assume that players can choose only from among a fixed finite set $X = \{\hat{x}_1, \ldots, \hat{x}_m\}$ of possible contributions. Under these two assumptions, the strategies of the players take the form of a vector $\boldsymbol{p} = (p_{0,k}, p_{\boldsymbol{x},k})$. The entries $p_{0,k}$ for $1 \leq k \leq m$ give the probability of the player to choose contribution level $\hat{x}_k$ in the first round, when no previous history is yet available. The other entries $p_{\boldsymbol{x},k}$ give the probability of the player to choose $\hat{x}_k$ in subsequent rounds, conditional on the contribution vector $\boldsymbol{x} \in X^n$ of the previous round. For $\boldsymbol{p}$ to be a sensible strategy, we require $\sum_{k=1}^{m} p_{0,k} = 1$ and $\sum_{k=1}^{m} p_{\mathbf{x},k} = 1$ for all $\boldsymbol{x}$; that is, the strategy must prescribe an action for any given outcome of the previous round. When all players apply memory-1 strategies, their payoffs in the repeated game can be computed efficiently by representing the game as a Markov chain. The algorithm is shown in the Supplementary Information.

In the special case that players can give only their full endowment or nothing at all, we obtain $X = \{0, 1\}$. We refer to these two possible actions as 'cooperation' (C) and 'defection' (D). When there are only these two possible contribution levels, we can drop the index k in the definition of a memory-1 strategy and write $\boldsymbol{p} = (p_0; p_{\boldsymbol{x}})$. Under this notation, p_z is now the probability that the player will cooperate in the next round. If the game involves only two players, we obtain the typical format of memory-1 strategies for the iterated prisoner's dilemma[3], $\boldsymbol{p} = (p_0; p_{CC}, p_{CD}, p_{DC}, p_{DD})$. For example, the strategy Grim may be approximated by the memory-1 strategy $\boldsymbol{p} = (1; 1, 0, 0, 0)$. In the absence of errors, this memory-1 strategy cooperates only if both players have cooperated in all previous rounds.

Pure memory-1 strategies have entries that are either zero or one. Given the outcome of the previous round, their action is deterministic. Stochastic memory-1 strategies have entries that can take arbitrary values between zero and one. For given m and n, there are finitely many pure memory-1 strategies, but infinitely many stochastic memory-1 strategies.

For our evolutionary analysis, the actions of the players may be subject to implementation errors. That is, if the set of possible contributions is $X = \{\hat{x}_1, \ldots, \hat{x}_m\}$ and the player decides to choose the contribution $\hat{x}_k$, then the player will instead make a different contribution $\hat{x}_l$ with probability $\varepsilon/(m-1)$. We refer to ε as the error rate of the players. For infinitely repeated games (with $\delta = 1$), errors have the useful mathematical property that they make the game dynamics ergodic. As a result, the payoffs of the players will be independent of the contribution of the players in the very first round. In that case, we no longer need to specify a player's initial contribution probability $p_{0,k}$.

To model how players adapt their memory-1 strategies over time, we introduce an evolutionary process that we call 'introspection dynamics'. For this process, we again consider n players who interact in an asymmetric public goods game. In each evolutionary time step, one of the players is chosen at random to revise their strategy. To this end, this player i considers a randomly chosen alternative memory-1 strategy. Suppose the original strategy yields payoff π_i, whereas the alternative strategy yields payoff $\tilde{\pi}_i$ (keeping the strategies of the other players fixed). Then player i switches to the alternative strategy with probability $\rho = \left(1 + e^{-s(\tilde{\pi}_i - \pi_i)}\right)^{-1}$. The parameter $s \geq 0$ represents the 'strength of selection'. In the limiting case $s \to 0$, the switching probability simplifies to $\rho = 1/2$, such that players adopt new strategies at random. In the other limiting case $s \to \infty$, the player adopts the alternative strategy only if it yields at least the payoff of their original strategy. Iterating these updates over many time steps, we obtain an ergodic process on the space of all strategy choices of n players. In particular, we note that this process has no absorbing states. Even if a strategy profile is an equilibrium, there is always a positive chance that one of the players deviates owing to chance. For small n, the invariant distribution of the evolutionary process can be calculated exactly. For larger n, the invariant distribution can be approximated by simulations.

Although memory-1 strategies have been routinely used to explore the evolution of reciprocity[41–63], it is natural to ask to what extent our results depend on the assumption of one-round memory. To explore this issue, we repeated all simulations with a more-general strategy space. We follow a previously published approach[15,64,65]. Players can choose among all strategies that can be represented by finite-state automata over the possible contributions X. Finite-state automata contain the previously considered memory-1 strategies as a special case. However, they can also encode strategies with arbitrarily long memory (Extended Data Fig. 6a). For the evolutionary process, we assume that when a mutation occurs, four cases can occur: (i) the action chosen in a given state changes, (ii) a transition between two states changes, (iii) a new state is added to the finite-state automaton or (iv) an existing state is removed (Extended Data Fig. 6b). Simulations show that although absolute cooperation rates tend to be lower for this strategy space, all of our qualitative predictions remain unchanged (Extended Data Fig. 6c). See Supplementary Information for details.

Experimental methods. For our experiment, we have recruited 436 participants on Amazon Mechanical Turk to take part in an interactive game. The experiment was implemented with SoPHIE, an online platform that allows for real-time interaction between participants on Amazon Mechanical Turk[10,66,67].

Participants were matched in pairs, which were randomly assigned to one of the five treatments. For each pair, one participant was randomly determined to adopt role A, whereas the other participant obtained role B. Players received US$1.00 for participating and could earn a bonus payment depending on their performance in the game. The tokens earned during the game were converted to US dollars at a rate of 800 tokens = US$1.00. The average bonus participants earned was US$1.70. After reading the experimental instructions (Supplementary Information), all participants had to pass a series of comprehension questions to ensure they understood the consequences of their decisions. All players were anonymous. They were identified only by their player ID (A or B). Each game consisted of at least 20 rounds. Thereafter, the game was continued with a 50% probability after each round to avoid end-game effects.

The behavioural experiment is based on the public goods game with the payoff function given by equation (1). Before the first round, both players were assigned an endowment e_i and a productivity value r_i. The possible values of e_i and r_i are depicted in Fig. 4a. Once assigned, the e_i and r_i of each participant remained constant throughout the experiment. Both players were informed about their own and the other player's endowment and productivity. Each round, participants decided how much to contribute to the public good. They could contribute any integer between 0 and e_i. A player's absolute contribution was multiplied by the respective productivity value r_i. All multiplied contributions were split equally among the players. Participants could not observe the other player's contribution before making their own decision. However, after each round, participants learned each other's contributions as well as the resulting payoffs for each player.

We analysed the data using two-tailed non-parametric tests, using pairs of two interacting players as our statistical unit. That is, for each quantity of interest, we calculated the respective average value for each pair of players; then we compared this average value across treatments (Fig. 4) or within each treatment (Extended Data Figs. 7, 10). For comparisons between treatments, we use the Mann–Whitney U-test, whereas for comparisons within a treatment we use the Wilcoxon signed-rank test. In the main text and all figures, we report the outcome of each test directly, without correcting for multiple testing. However, all of our key findings continue to hold when we apply Bonferroni correction (Supplementary Information section 5.3).

The sample size was determined in advance based on similar past research[10]. The number of groups that completed the experiment were $n_1 = 42$, $n_2 = 42$, $n_3 = 40$, $n_4 = 39$, $n_5 = 40$ for each of the five treatments, respectively. We find no significant differences between groups that completed the experiment and groups for which at least one player dropped out (Supplementary Information). For the statistical results presented in the main text, we used only the first 20 rounds of groups that completed the experiment. However, all of our conclusions remain valid if we include dropout groups by using multiple imputation (Supplementary Tables 1, 2).

In the Supplementary Information, we provide a full description of the methods used, and we report all test statistics and P values. Moreover, we discuss further aspects of our empirical results, such as the game dynamics over time or the distribution of contributions (Extended Data Figs. 7–10).

Parameters used for figures. Figure 2a–c shows the region in the endowment space in which full cooperation is feasible. The respective calculations are provided in the Supplementary Information. The first two columns are based on the linear public goods game with parameters $r_1 = r_2 = r_3 = 2$, $\delta = 0.8$ (Fig. 2a) and $r_1 = 2.9$, $r_2 = 1.5$, $r_3 = 1.1$, $\delta = 0.3$ (Fig. 2b), respectively. The last column considers a nonlinear three-player public goods game with $\delta = 0.35$ (Fig. 2c) and payoff function

$$u_i(\boldsymbol{e}, \boldsymbol{x}) = \frac{1}{2}\max_{j,\, k\neq j}(e_j x_j + e_k x_k) + \frac{1}{3}\sum_{j=1}^{3} e_j x_j + (1-x_i)e_i \quad (5)$$

This game represents a situation in which the two highest absolute contributions are of particular importance for the public good.

Figure 2d–f shows the outcome of evolutionary simulations. We systematically varied the players' initial endowments, considering all endowment distributions (e_1, e_2, e_3) for which $e_i \in \{0.00, 0.05, \ldots, 0.95, 1.00\}$. We used the same three payoff functions as in Fig. 2a–c, a continuation probability of $\delta = 1$ and strong selection, $s = 1{,}000$. Players use stochastic memory-1 strategies without errors, and they either contribute their full endowment or nothing, $X = \{0, 1\}$. The evolutionary process was simulated for 10^6 elementary time steps.

Figure 3 shows simulations as we vary player 1's endowment $e_1 \in \{0.00, 0.05, \ldots, 1.00\}$ and $e_2 = 1 - e_1$. We use the same productivity values as in the experiment, $r_1 = r_2 = 1.6$ (Fig. 3a) or $r_1 = 1.9$ and $r_2 = 1.3$ (Fig. 3b), respectively, and consider the case $\delta = 1$ and $s = 1{,}000$. To explore the robustness of our evolutionary findings, we consider three different scenarios, depending on the possible contribution levels in each round, $X_1 = \{0, 1\}$, $X_2 = \{0, 1/2, 1\}$ and $X_3 = \{0, 1/3, 2/3, 1\}$. Players can choose among all pure memory-1 strategies, subject to an error rate of $\varepsilon = 0.001$. For each value of e_1, simulations were run for at least 2×10^6 time steps for each data point.

Extended Data Figures 1–4 show further evolutionary results for the pairwise game considered in the behavioural experiment. For these figures, we assume that players choose only among pure memory-1 strategies with errors, and that they contribute only their full endowment or nothing in any given round. As a consequence, there are 16 possible strategies $\boldsymbol{p} = (p_{CC}, p_{CD}, p_{DC}, p_{DD})$. For example, the strategy of unconditional defectors is given by ALLD = (0, 0, 0, 0), whereas WSLS[3] takes the form WSLS = (1, 0, 0, 1). For these 16 strategies, we can compute numerically exact strategy abundances (Supplementary Information). Except for the parameters explicitly varied, all payoff parameters are the same as in the five experimental treatments, using a continuation probability $\delta = 1$, selection strength $s = 1{,}000$ and error rate $\varepsilon = 0.05$.

Extended Data Figure 5 considers a public goods game in which players have the same productivity, but they yield different benefits from the public goods. The payoff function is given by

$$u_i(\boldsymbol{e}, \boldsymbol{x}) = q_i r \sum_j x_j e_j + (1-x_i)e_i \quad (6)$$

Here, r is the common productivity of the players and $q_i \in [0, 1]$ is player i's share of the public good. The game is a social dilemma only for certain values of q_i (see Supplementary Information for details). We show numerically exact results for pure memory-1 strategies with errors, and possible contribution levels $X = \{0, 1\}$. We use the parameters $r = 1.6$, $s = 1{,}000$ and $\varepsilon = 0.05$.

For Extended Data Fig. 6, we repeat the simulations shown in Fig. 3 for the case in which players can choose their strategies from the set of finite-state automata. We use the same baseline parameters as in Fig. 3. However, simulations are run for longer (5×10^6 time steps) and the error rate has been set to $\varepsilon = 0$ to allow for neutral invasions as previously described[15,64,65].

The results of our behavioural experiment are shown in Fig. 4 and Extended Data Figs. 7–10. As auxiliary information, we also provide error bars that indicate the respective 95% confidence intervals in Fig. 4 and Extended Data Figs. 7, 10. For the theoretical predictions, we used simulations for stochastic memory-1 strategies and possible contributions $x \in \{0, 1\}$. As parameters, we chose $s = 1{,}000$ and $\varepsilon = 0.001$. As indicated in Fig. 3 and Extended Data Fig. 4, our qualitative predictions are independent of the evolutionary parameters that we use, and independent of the possible contribution levels. A detailed description of the methods applied and of the depicted results is provided in the Supplementary Information.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

Data availability

The experimental data on which Fig. 4 and Extended Data Figs. 7–10 are based, as well as the STATA and R files that contain our statistical analysis, are available at https://osf.io/92jyw/.

Code availability

All evolutionary simulations and numerical calculations have been performed with MATLAB R2014A. We provide the respective scripts in the Supplementary Information. These scripts can be used to compute the payoffs of the players, to simulate the introspection dynamics and to numerically compute the expected dynamics.

31. Milinski, M., Sommerfeld, R. D., Krambeck, H.-J., Reed, F. A. & Marotzke, J. The collective-risk social dilemma and the prevention of simulated dangerous climate change. *Proc. Natl Acad. Sci. USA* **105**, 2291–2294 (2008).
32. Pacheco, J. M., Santos, F. C., Souza, M. O. & Skyrms, B. Evolutionary dynamics of collective action in *N*-person stag hunt dilemmas. *Proc. R. Soc. B* **276**, 315–321 (2009).
33. Jacquet, J. et al. Intra- and intergenerational discounting in the climate game. *Nat. Clim. Change* **3**, 1025–1028 (2013).
34. Vasconcelos, V. V., Santos, F. C. & Pacheco, J. M. A bottom-up institutional approach to cooperative governance of risky commons. *Nat. Clim. Change* **3**, 797–801 (2013).
35. Archetti, M. & Scheuring, I. Review: game theory of public goods in one-shot social dilemmas without assortment. *J. Theor. Biol*. **299**, 9–20 (2012).
36. Milinski, M., Röhl, T. & Marotzke, J. Cooperative interaction of rich and poor can be catalyzed by intermediate climate targets. *Clim. Change* **109**, 807–814 (2011).
37. Vasconcelos, V. V., Santos, F. C., Pacheco, J. M. & Levin, S. A. Climate policies under wealth inequality. *Proc. Natl Acad. Sci. USA* **111**, 2212–2216 (2014).
38. Abou Chakra, M. & Traulsen, A. Under high stakes and uncertainty the rich should lend the poor a helping hand. *J. Theor. Biol*. **341**, 123–130 (2014).
39. Abou Chakra, M., Bumann, S., Schenk, H., Oschlies, A. & Traulsen, A. Immediate action is the best strategy when facing uncertain climate change. *Nat. Commun*. **9**, 2566 (2018).
40. Hauser, O. P., Traulsen, A. & Nowak, M. A. Heterogeneity in background fitness acts as a suppressor of selection. *J. Theor. Biol*. **343**, 178–185 (2014).
41. Akin, E. What you gotta know to play good in the Iterated Prisoner's Dilemma. *Games* **6**, 175–190 (2015).
42. Nowak, M. A. & Sigmund, K. Tit for tat in heterogeneous populations. *Nature* **355**, 250–253 (1992).
43. Frean, M. R. The prisoner's dilemma without synchrony. *Proc. R. Soc. Lond. B* **257**, 75–79 (1994).
44. Killingback, T., Doebeli, M. & Knowlton, N. Variable investment, the Continuous Prisoner's Dilemma, and the origin of cooperation. *Proc. R. Soc. Lond. B* **266**, 1723–1728 (1999).
45. Imhof, L. A. & Nowak, M. A. Stochastic evolutionary dynamics of direct reciprocity. *Proc. R. Soc. B* **277**, 463–468 (2010).
46. Kurokawa, S., Wakano, J. Y. & Ihara, Y. Generous cooperators can outperform non-generous cooperators when replacing a population of defectors. *Theor. Popul. Biol*. **77**, 257–262 (2010).
47. García, J. & Traulsen, A. The structure of mutations and the evolution of cooperation. *PLoS ONE* **7**, e35287 (2012).
48. Grujić, J., Cuesta, J. A. & Sánchez, A. On the coexistence of cooperators,defectors and conditional cooperators in the multiplayer iterated Prisoner's Dilemma. *J. Theor. Biol*. **300**, 299–308 (2012).
49. Press, W. H. & Dyson, F. J. Iterated Prisoner's Dilemma contains strategies that dominate any evolutionary opponent. *Proc. Natl Acad. Sci. USA* **109**, 10409–10413 (2012).
50. Van Segbroeck, S., Pacheco, J. M., Lenaerts, T. & Santos, F. C. Emergence of fairness in repeated group interactions. *Phys. Rev. Lett*. **108**, 158104 (2012).
51. Akin, E. in *Ergodic Theory, Advances in Dynamics* (ed. Assani, I.) 77–107 (de Gruyter, Berlin, 2016).
52. Stewart, A. J. & Plotkin, J. B. Collapse of cooperation in evolving games. *Proc. Natl Acad. Sci. USA* **111**, 17558–17563 (2014).
53. Stewart, A. J. & Plotkin, J. B. The evolvability of cooperation under local and non-local mutations. *Games* **6**, 231–250 (2015).
54. Szolnoki, A. & Perc, M. Defection and extortion as unexpected catalysts of unconditional cooperation in structured populations. *Sci. Rep*. **4**, 5496 (2014).
55. Toupo, D. F. P., Rand, D. G. & Strogatz, S. H. Limit cycles sparked by mutation in the repeated prisoner's dilemma. *Int. J. Bifurc. Chaos* **24**, 1430035 (2014).
56. Dong, Y., Li, C., Tao, Y. & Zhang, B. Evolution of conformity in social dilemmas. *PLoS ONE* **10**, e0137435 (2015).
57. Pan, L., Hao, D., Rong, Z. & Zhou, T. Zero-determinant strategies in iterated public goods game. *Sci. Rep*. **5**, 13096 (2015).
58. Baek, S. K., Jeong, H. C., Hilbe, C. & Nowak, M. A. Comparing reactive and memory-one strategies of direct reciprocity. *Sci. Rep*. **6**, 25676 (2016).
59. McAvoy, A. & Hauert, C. Autocratic strategies for iterated games with arbitrary action spaces. *Proc. Natl Acad. Sci. USA* **113**, 3573–3578 (2016).
60. Reiter, J. G., Hilbe, C., Rand, D. G., Chatterjee, K. & Nowak, M. A. Crosstalk in concurrent repeated games impedes direct reciprocity and requires stronger levels of forgiveness. *Nat. Commun*. **9**, 555 (2018).
61. Ichinose, G. & Masuda, N. Zero-determinant strategies in finitely repeated games. *J. Theor. Biol*. **438**, 61–77 (2018).
62. Hilbe, C., Chatterjee, K. & Nowak, M. A. Partners and rivals in direct reciprocity. *Nat. Hum. Behav*. **2**, 469–477 (2018).
63. Hilbe, C., Šimsa, Š., Chatterjee, K. & Nowak, M. A. Evolution of cooperation in stochastic games. *Nature* **559**, 246–249 (2018).
64. García, J. & van Veelen, M. In and out of equilibrium I: evolution of strategies in repeated games with discounting. *J. Econ. Theory* **161**, 161–189 (2016).
65. García, J. & van Veelen, M. No strategy can win in the repeated Prisoner's Dilemma: linking game theory and computer simulations. *Front. Robot. AI* **5**, 102 (2018).
66. Hendriks, A. *SoPHIE — Software Platform for Human Interaction Experiments*. https://www.sophie.uni-osnabrueck.de/start/ (2012).
67. Hauser, O. P., Hendriks, A., Rand, D. G. & Nowak, M. A. Think global, act local: preserving the global commons. *Sci. Rep*. **6**, 36079 (2016).

Acknowledgements This work was supported by the European Research Council Start Grant 279307: Graph Games (to K.C.), Austrian Science Fund (FWF) NFN Grant S11407-N23 Rigorous Systems Engineering/Systematic Methods in Systems Engineering (to K.C.), Office of Naval Research Grant N00014-16-1-2914 (to M.A.N.), Defense Advanced Research Projects Agency Grant W911NF-18-2-0265 (to M.A.N.), and the John Templeton Foundation Grant 55832 (to M.A.N.). C.H. acknowledges support from the ISTFELLOW program.

Author contributions All authors conceived the study, performed the analysis, discussed the results and wrote the manuscript.

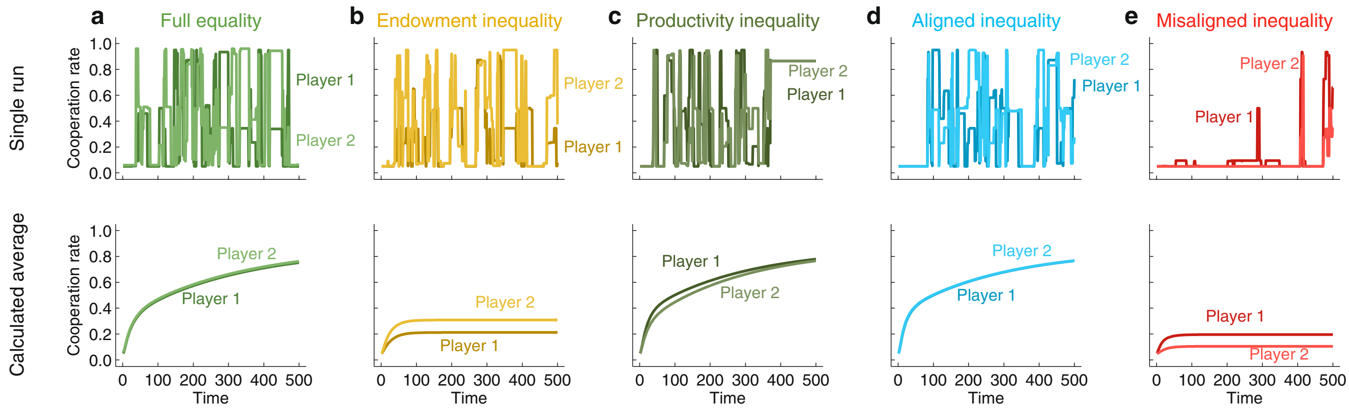
Competing interests The authors declare no competing interests.

Additional information

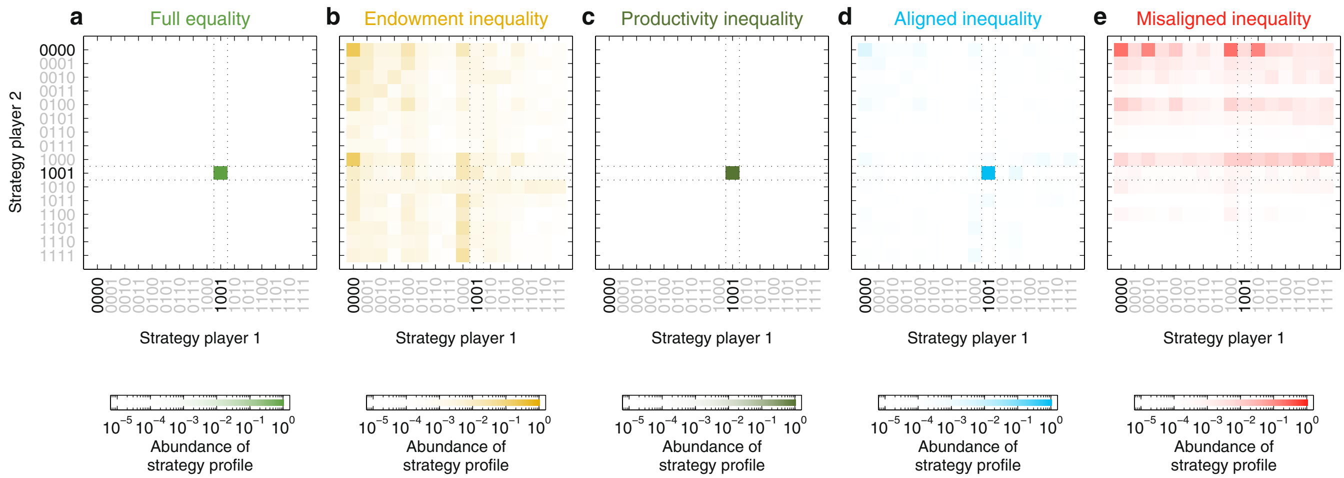
Supplementary information is available for this paper at https://doi.org/10.1038/s41586-019-1488-5.

Correspondence and requests for materials should be addressed to O.P.H. or C.H. or M.A.N.

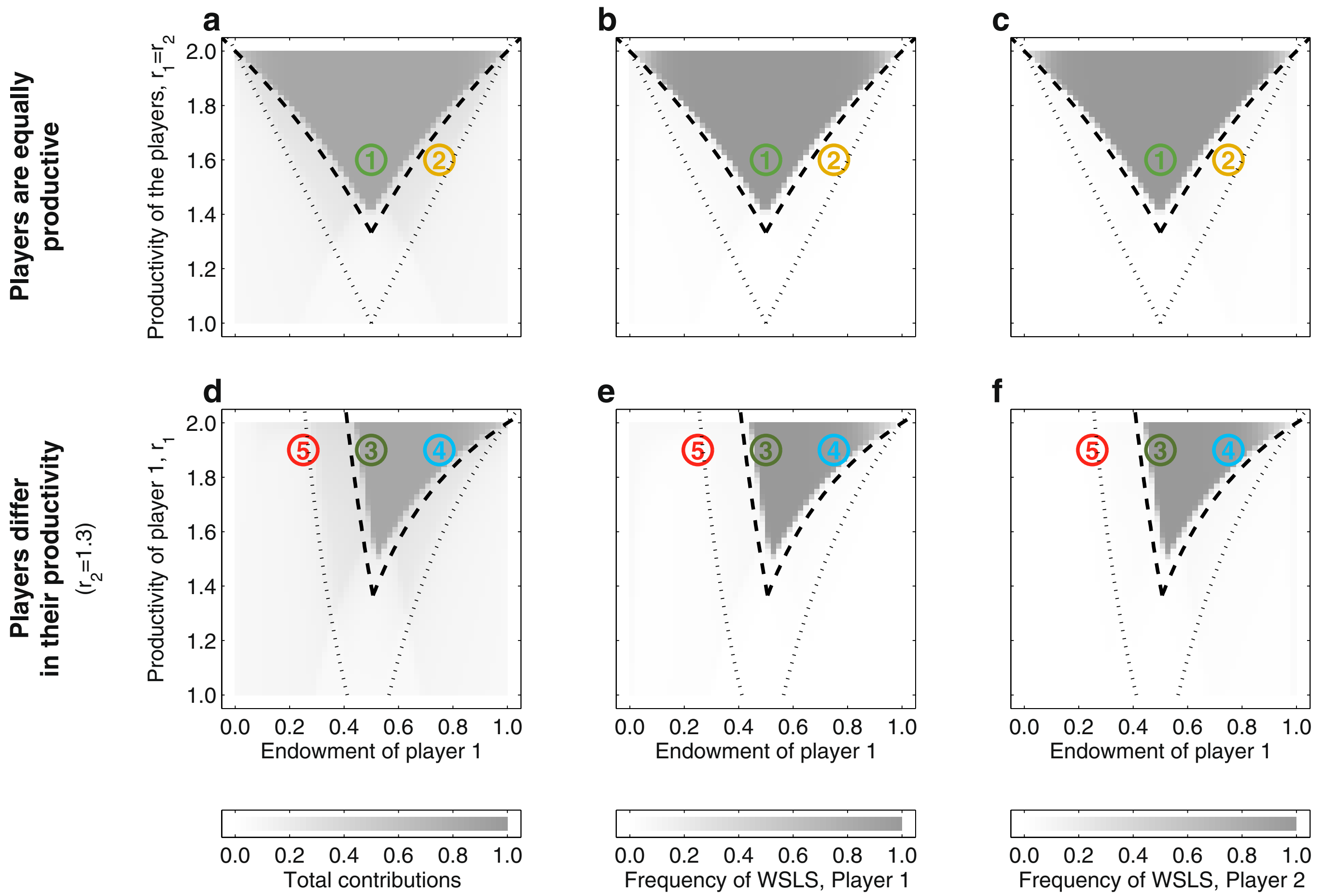
Peer review information *Nature* thanks Joe Yuichiro Wakano and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.



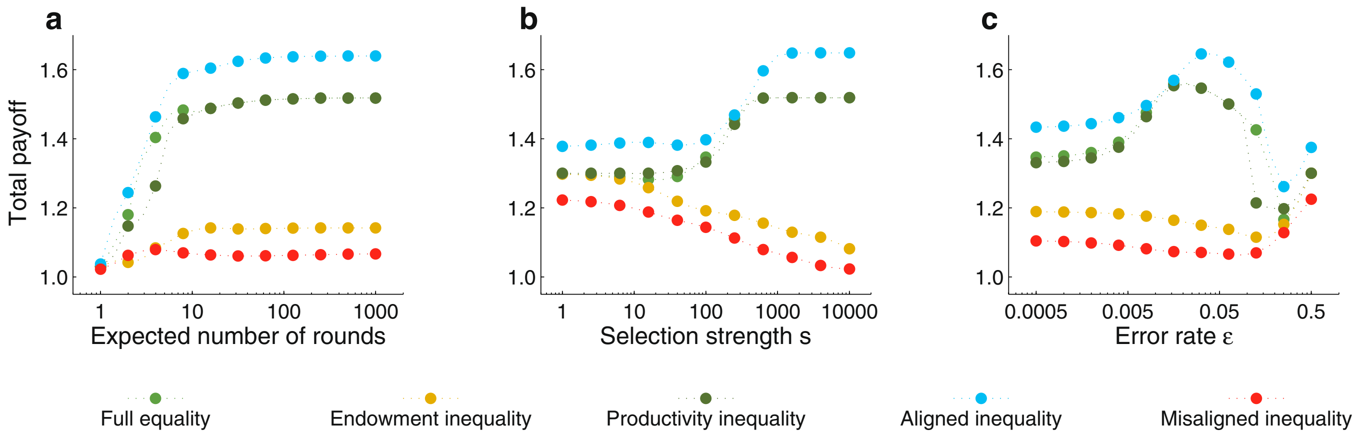
Extended Data Fig. 1 | Dynamics of cooperation among unequals. In Figs. 2, 3, we show how often players cooperate on average. **a**–**e**, Here we depict evolutionary trajectories over time, for the five treatments considered in our experiment. We assume that players can choose among the 16 pure memory-1 strategies. Top, five single runs of the introspection dynamics. Bottom, expected trajectories of the introspection dynamics, which can be derived explicitly (Supplementary Information section 4.3). These expected trajectories represent the cooperation rate over time as we average over many realizations of the process. We observe substantial cooperation in three of the five cases: in the treatments with full equality (**a**), productivity inequality (**c**) and aligned inequality (**d**).



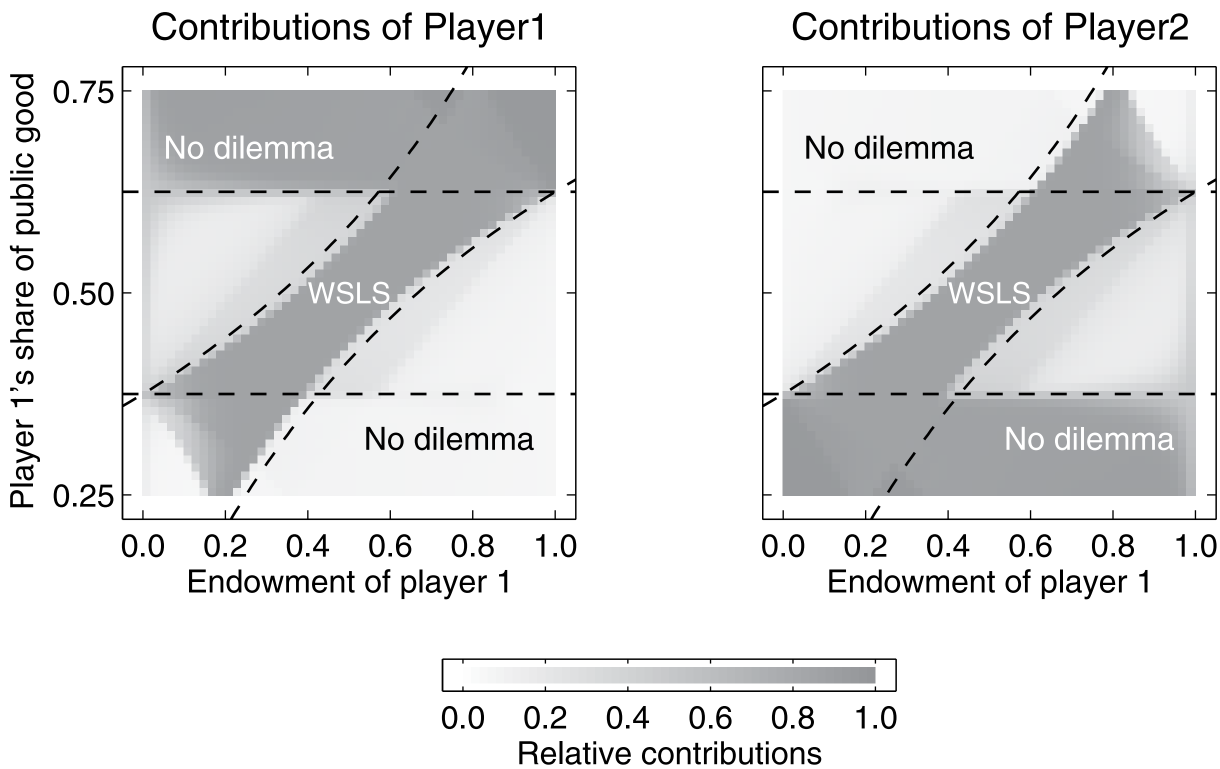
Extended Data Fig. 2 | Under endowment inequality and misaligned inequality, players fail to coordinate on WSLS. Here, we consider the long-run dynamics of the games considered in Extended Data Fig. 1. For each pair ($\boldsymbol{p}_1$, $\boldsymbol{p}_2$) of pure memory-1 strategies, we can compute how often the respective strategy pair is played according to the invariant distribution of the evolutionary process. **a**, **c**, **d**, Under full equality, productivity inequality or aligned inequality, players typically coordinate on a WSLS equilibrium, as indicated by the coloured square in the centre of the dotted lines. **b**, **e**, Under endowment inequality or misaligned inequality, players fail to coordinate on a unique equilibrium. Instead, most of the evolving strategies prescribe to defect against the opponent. We note that in those treatments in which players have different endowments, the low-endowment player faces a reduced strength of selection (because the endowment of this player is reduced from 0.5 to 0.25). As a consequence, the marginal distribution of the low-endowment player in **b**, **e** is more uniform than the marginal distribution of the high-endowment player.



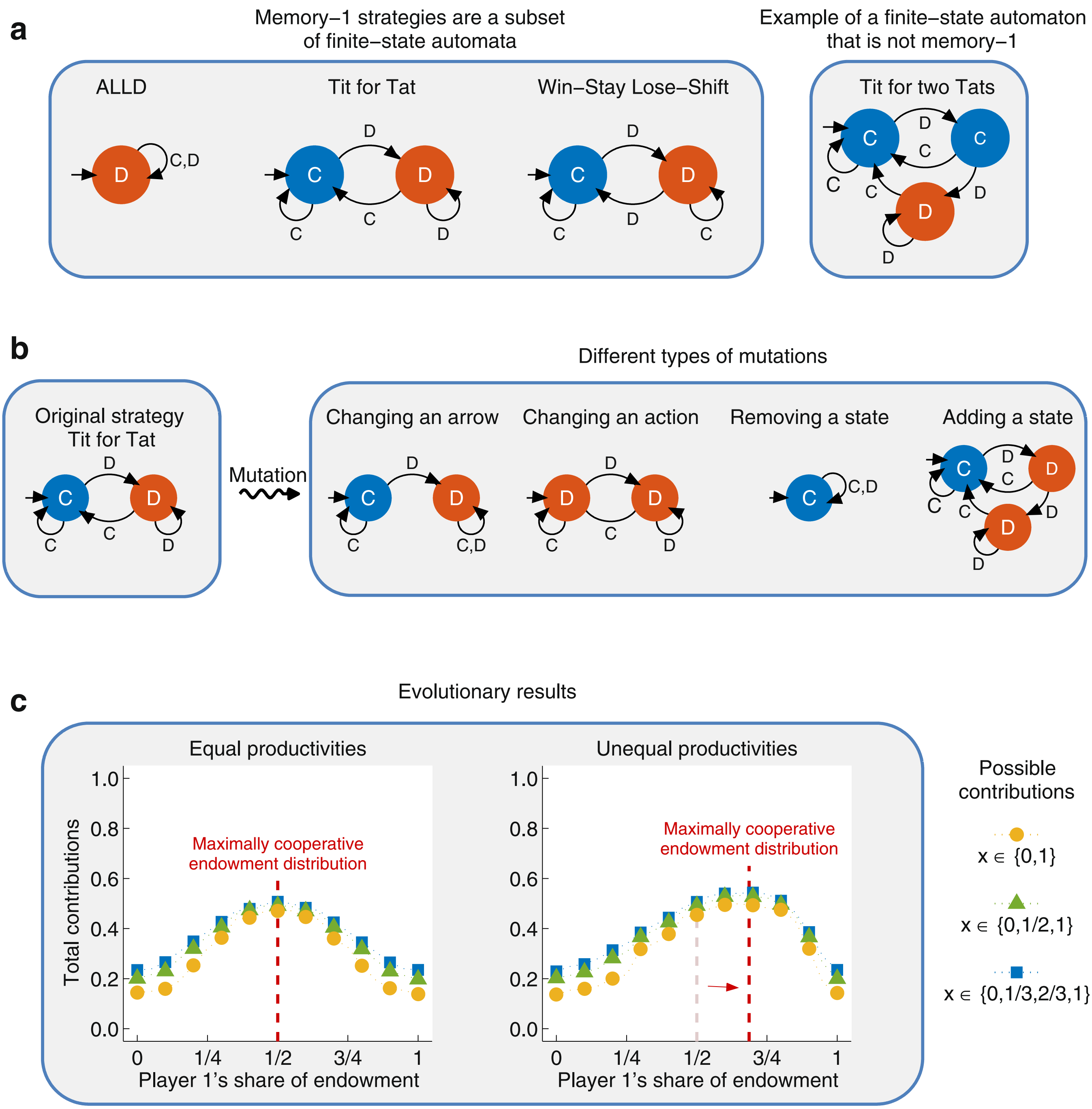
Extended Data Fig. 3 | An equilibrium analysis explains why cooperation emerges in only three of the five treatments. Using the same two-player setup as in Extended Data Figs. 1, 2, we explored how much players contribute on average when we simultaneously vary the endowment (*x* axis) as well as their productivity r_1 of player 1. For each parameter combination, we record the total contributions of the player and how often they use WSLS according to the invariant distribution of the evolutionary process (indicated in shades of grey). We compare these evolutionary results with the region for which WSLS is an equilibrium (indicated by dashed lines) and with the region for which Grim is an equilibrium (dotted lines); see Supplementary Information for details. The coloured symbols indicate which parameter combinations have been used for the experimental treatments. **a**–**c**, For equal productivities, the full equality treatment (1) is in the region in which cooperation can evolve, whereas the unequal endowment treatment (2) is not. **d**–**f**, For unequal productivities, only the misaligned inequality treatment (5) is outside the region in which cooperation can evolve.



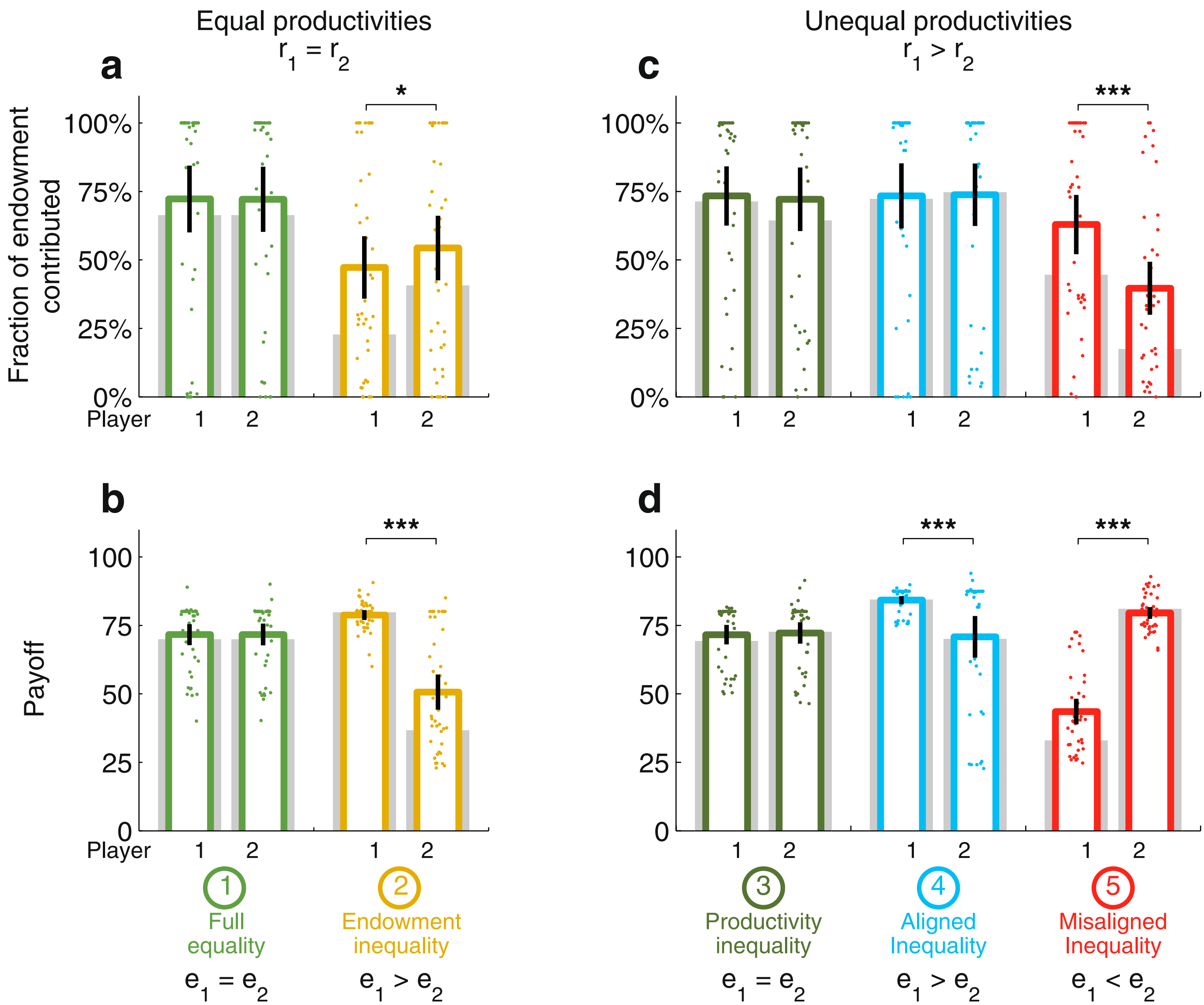
Extended Data Fig. 4 | Robustness of evolutionary results with respect to parameter changes. a–c, To explore the robustness of our theoretical predictions, we varied the expected number of rounds played between two players (**a**), the selection strength (**b**) and the rate at which players commit an implementation error (**c**). Although the quantitative results depend on these parameters, the qualitative ordering of the five treatments is the same across all considered scenarios. Except for the parameters explicitly varied on the *x* axis, all parameters are the same as in Extended Data Figs. 1, 2.



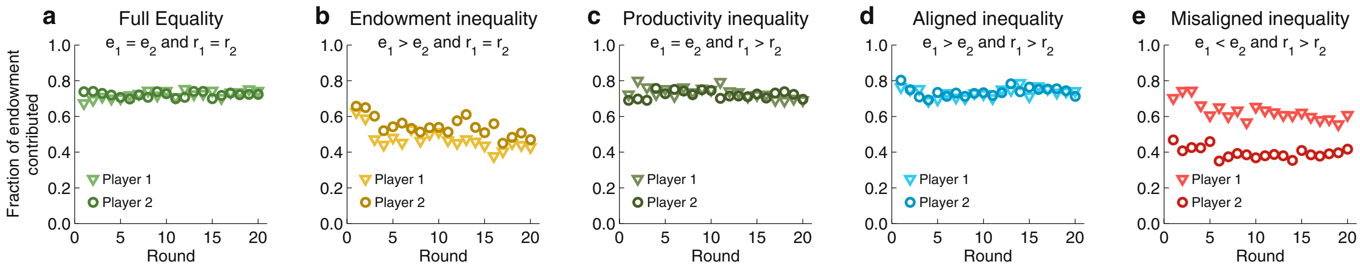
Extended Data Fig. 5 | Cooperation in an asymmetric game in which players derive different payoffs from the public good. Instead of considering players who differ in their productivity, here we consider an asymmetric two-player public goods game in which players differ in the share of the public goods that they get (the exact model is specified in the Supplementary Information). We vary two parameters, player 1's share of the initial endowment, and player 1's share of the public good. For each parameter combination, we record the average contributions of the players over the course of the evolutionary process (indicated in the grey colour). For games in which players get different shares of the public good, we note that the game is a social dilemma only if neither player's share is too large (otherwise that player would always have an incentive to cooperate, no matter what the co-player does). However, if both players get an intermediate share of the public good, full cooperation can again evolve when WSLS is an equilibrium.



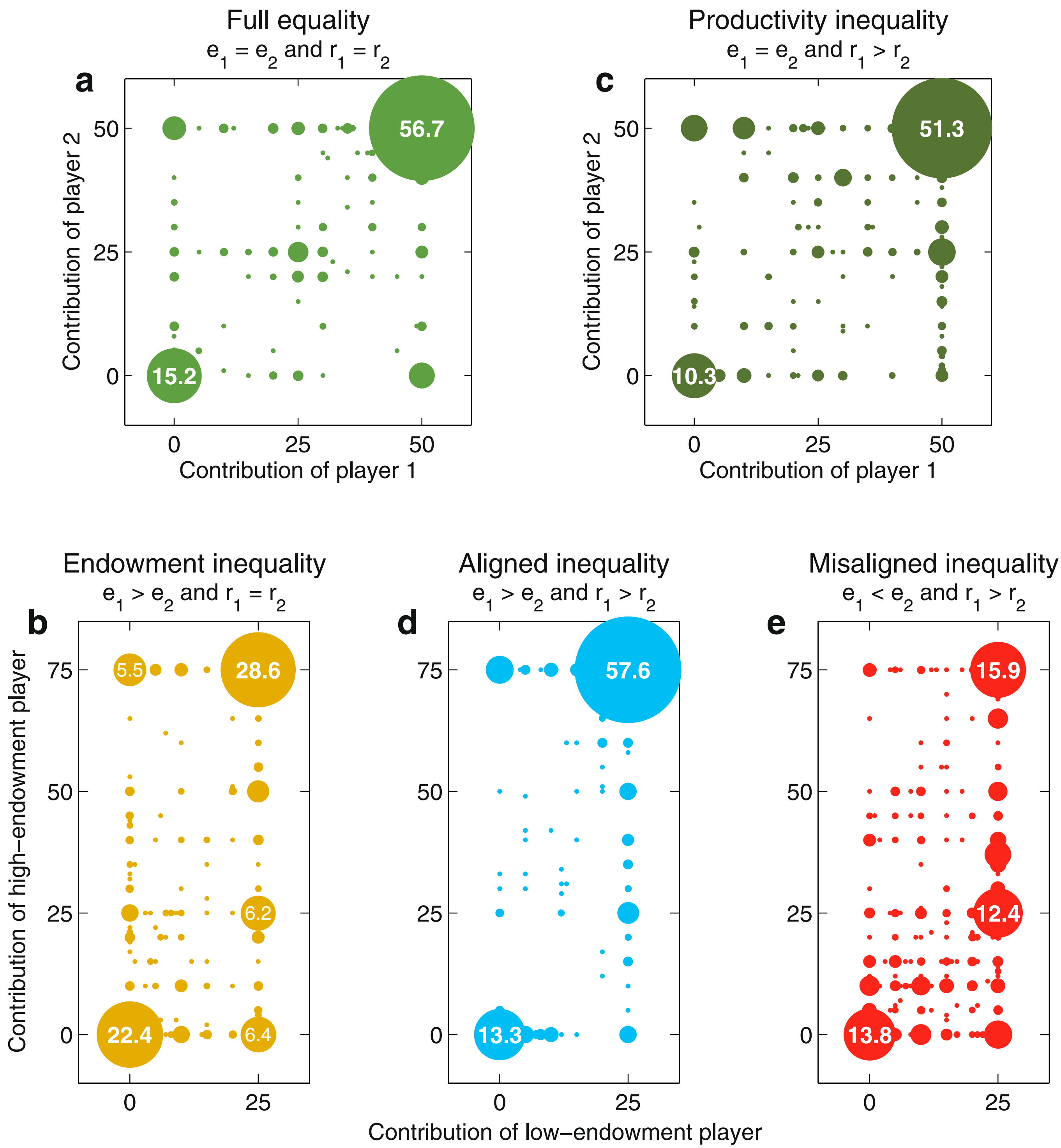
Extended Data Fig. 6 | Evolution of cooperation among players using finite-state automata. a, Here we represent finite-state automata for a game between two players in which players can either contribute their full endowment (C) or nothing (D). A finite-state automaton consists of three components: a set of states (represented by the large circles), the action played in each state (represented by the colour of the circle and the letters 'C' and 'D') and a transition rule (represented by arrows; the associated letter shows for which of the co-player's actions the respective arrow is taken). Finite-state automata are able to implement all memory-1 strategies. In addition, they can encode strategies that depend on arbitrarily long sequences of past actions. **b**, To model evolution among finite-state automata, we use a previously published mutation scheme[15,64]. When a mutation occurs, the direction of a random arrow is changed, the action in a randomly chosen state is changed, a random state is removed or a state is added. **c**, Using this more general strategy space, we repeated the simulations in Fig. 3. Although overall cooperation rates are slightly lower, all qualitative results remain unchanged.



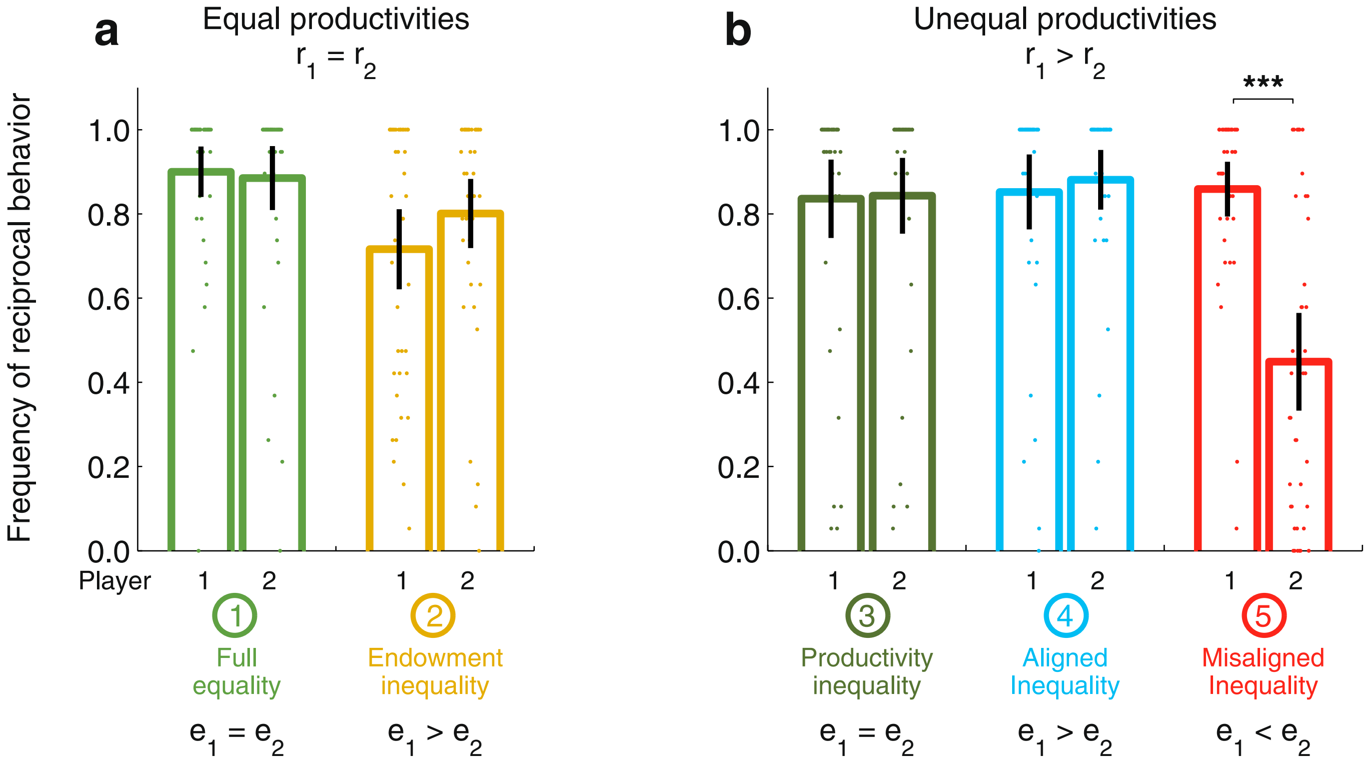
Extended Data Fig. 7 | Contributions and payoffs of the two players across treatments. For each of the five experimental treatments, we compare the average contributions and the average payoff of the two players. Grey bars indicate the theoretical prediction based on evolutionary simulations. Coloured bars depict the outcome of the experiment. Error bars represent the respective 95% confidence intervals. Asterisks indicate statistical differences based on two-tailed Wilcoxon signed-rank tests. The number of groups per treatment is 42, 42, 40, 39, 40 for treatments 1–5, respectively. **a**, **b**, Under full equality, the two players contribute a similar share of their endowment and they obtain approximately equal payoffs. Under endowment inequality, the cooperation rates of both players are reduced, with the contributions of the high-endowment player (player 1) being significantly lower than the contributions of player 2. **c**, **d**, For productivity inequality and aligned inequality, we find no differences in the relative contributions of the players. For misaligned inequality, the relative contributions of the better-endowed but less-productive player 2 are considerably reduced. For both aligned and misaligned inequality, the two players earn significantly different payoffs. Nevertheless, the player with the lower payoff in the aligned inequality treatment derives a similar payoff as the two player types under productivity inequality. For details, see Supplementary Information.



Extended Data Fig. 8 | Experimental dynamics of cooperation. **a**–**e**, For each of the five treatments, we show the average contributions of the players over the course of the experiment. In all treatments the contributions are relatively stable over time, except for a significant negative trend in the treatment with endowment inequality (**b**) (see Supplementary Information for details).



Extended Data Fig. 9 | Individual cooperation decisions across the five treatments. a–e, To analyse the joint contribution decisions of the two players, we plot here how often player 1 has contributed y_1 tokens while player 2 has contributed y_2 tokens, for each pair (y_1, y_2). **a**, **c**, **d**, Under full equality (**a**), productivity inequality (**c**) and aligned inequality (**d**), most individual decisions are mutually cooperative. **b**, **e**, By contrast, under endowment inequality (**b**) and misaligned inequality (**e**), contributions are more scattered. **e**, Moreover, in the treatment with misaligned inequality, we observe that a substantial fraction of high-endowment players only matches the absolute contributions of the other player. For example, in 12.4% of the rounds, the low-endowment player contributes all 25 tokens at their disposal, and the high-endowment player contributes the same absolute amount of tokens (corresponding to 1/3 of this player's endowment).



Extended Data Fig. 10 | Abundance of reciprocal behaviours across the five treatments. a, **b**, To explore whether subjects apply reciprocal strategies, we show the fraction of rounds in which subjects match or exceed their co-player's relative contribution from the previous round. That is, if player 1 has contributed x% of their endowment in round t, we record whether or not player 2 contributes at least x% of their endowment in round $t+1$. Note that reciprocal strategies do not automatically yield high cooperation rates, because mutually defecting players are also reciprocal. Error bars represent the respective confidence intervals. Statistically significant differences were analysed using a two-tailed Wilcoxon signed-rank test. $***P < 0.001$. Sample sizes are 42, 42, 40, 39, 40 for the treatments 1–5, respectively. Generally, we find high levels of reciprocity; only in the treatment with misaligned inequality does the high-endowment low-productivity player 2 exhibit a strongly reduced reciprocity rate. See Supplementary Information for details.

nature research

Corresponding author(s): Martin A. Nowak

Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see Authors & Referees and the Editorial Policy Checklist.

Statistical parameters

When statistical analyses are reported, confirm that the following items are present in the relevant location (e.g. figure legend, table legend, main text, or Methods section).

n/a	Confirmed	
☐	☒	The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	An indication of whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☒	☐	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistics including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒	Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated
☐	☒	Clearly defined error bars *State explicitly what error bars represent (e.g. SD, SE, CI)*

Our web collection on statistics for biologists may be useful.

Software and code

Policy information about availability of computer code

Data collection	All evolutionary simulations were performed using Matlab R2014A. The online experiment was implemented with SoPHIE, an online platform that allows for real-time interaction between Amazon Mechanical Turk (AMT) participants.
Data analysis	To analyze the experimental data, we used Stata SE 15.1, R 1.1.453, and Microsoft Excel 14.7.7.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

The data is publicly available on OSF: https://osf.io/92jyw/

Field-specific reporting

Please select the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/authors/policies/ReportingSummary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Participants were matched in pairs, which were assigned to one of five conditions (as described in Fig. 4a). The conditions varied across two dimensions: equality or inequality in endowments and equality or inequality in productivities. The five conditions are (1) Full equality in both dimensions, (2) Endowment inequality only, (3) Productivity inequality only, (4) Aligned inequality (the more productive player has a higher endowment), (5) Misaligned inequality (the more productive player has a lower endowment). Each pair of players interacted over at least 20 rounds. After that, the game was repeated with 50% probability after each round. See SI Section 5.1 for details. Because of the repeated interaction between two players, the data is structured hierarchically. For the main analysis, we averaged the two players' contributions at the round level and subsequently at the group level. The experiment was conducted exactly once. The number of participants for each condition is described below.
Research sample	We recruited N = 436 participants on Amazon Mechanical Turk (AMT).
Sampling strategy	The sample size was determined in advance based on similar past research (e.g. Hauser et al, Behavioral Public Policy, 2019). In total, we recruited 88, 88, 86, 86, and 88 subjects to participate in the five conditions, respectively. The number of subjects that completed the experiment was 84, 84, 80, 78, and 80, respectively. See SI Section 5 for details. The number of groups sampled has not been based on a formal power analysis. However, we chose our sample size such that we have a comparably large number of groups per condition, relative to previous studies on direct reciprocity (e.g. Wedekind and Milinski, PNAS 1996; Milinski and Wedekind, PNAS 1998; Dal Bo and Frechette, Am Econ Rev 2011; Fudenberg et al, Am Econ Rev 2012; Hilbe et al, Nature Communications 2015).
Data collection	The data was collected using SoPHIE, an online experimental software. Once the experiment is programmed and launched, data collection proceeds automatically. Once the data collection is completed, we downloaded the data for analysis offline.
Timing and spatial scale	Our experiments were conducted across 10 experimental sessions on AMT in October 2015.
Data exclusions	As planned from the outset, we only statistically analyzed the first twenty rounds of each game, because this was the maximum number of rounds all groups had in common. Moreover, we excluded groups in which at least one participant dropped out half-way through the game. However, all our results are unchanged when we use imputed values for dropout groups. See SI Section 5.3 for details.
Reproducibility	The experiment was conducted only once; however, our sample size is sufficiently large (and perhaps larger then usual) for experimental games of this nature.
Randomization	Randomization occurred at the session level.
Blinding	Blinding was not necessary because the experimental software took care of randomization and data collection automatically.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

Materials & experimental systems

n/a	Involved in the study
☒	☐ Unique biological materials
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☒	☐ Animals and other organisms
☐	☒ Human research participants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Human research participants

Policy information about studies involving human research participants

Population characteristics	Our study population is drawn from the general Amazon Mechanical Turk (see above) pool, which has been described in detail in other research (e.g. see Buhrmester et al. 2011)
Recruitment	Participants were recruited on AMT through a standard procedure by describing the nature of this research, the length of the task, the payoff for participating, and the potential for an additional bonus payment depending on decisions made during the study. For details, see SI Section 5.1.