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A novel route to cyclic dominance in voluntary social dilemmas

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Cooperation is the backbone of modern human societies, making it a priority to understand how successful cooperation-sustaining mechanisms operate. Cyclic dominance, a non-transitive set-up comprising at least three strategies wherein the first strategy overrules the second, which overrules the third, which, in turn, overrules the first strategy, is known to maintain biodiversity, drive competition between bacterial strains, and preserve cooperation in social dilemmas. Here, we present a novel route to cyclic dominance in voluntary social dilemmas by adding to the traditional mix of cooperators, defectors and loners, a fourth player type, risk-averse hedgers, who enact tit-for-tat upon paying a hedging cost to avoid being exploited. When this cost is sufficiently small, cooperators, defectors and hedgers enter a loop of cyclic dominance that preserves cooperation even under the most adverse conditions. By contrast, when the hedging cost is large, hedgers disappear, consequently reverting to the traditional interplay of cooperators, defectors, and loners. In the interim region of hedging costs, complex evolutionary dynamics ensues, prompting transitions between states with two, three or four competing strategies. Our results thus reveal that voluntary participation is but one pathway to sustained cooperation via cyclic dominance.

1. Introduction

Large-scale cooperation is a basis for solving key societal problems including climate inaction [1,2], resource overexploitation [3–5], imperfect vaccination [6–9], antibiotic overuse [10], crime occurrence [11], and epidemic outbreaks [12,13]. Cooperativeness as an altruistic act [14] entails a cost for the actor in order for the recipient to enjoy a benefit. Cooperators are, therefore, fundamentally challenged by the most basic principles of Darwinian evolution, i.e. why should anyone act selflessly if only the fittest succeed? This puzzle has mobilized an unprecedented spectrum of researchers across disciplines to seek out mechanisms that sustain and/or promote cooperation [14–21].

Social dilemmas, a construct of evolutionary game theory [22–24], capture the essence of the cooperation puzzle by contrasting individual and collective interests [25–28]. An important subclass of social dilemmas is the voluntary social dilemma [29,30], in which loners shape the evolutionary dynamics alongside traditional cooperators and defectors. Loners are risk averse, and to avoid getting exploited they resort to an exceedingly simple strategy that generates a small fixed income regardless of what their opponents do. This prompts the emergence of cyclic dominance, whereby cooperators dominate loners, who dominate defectors, who dominate cooperators, thus sustaining cooperation while strategy abundances keep oscillating [31]. Cyclic dominance emerges elsewhere too, e.g. in the public goods game with correlated punishment and reward [32], in the ultimatum game with discrete strategies [33], in social dilemmas with jokers [34], and by means of coevolution [35,36].

Cyclic dominance is often employed to study biodiversity [37–45] and competition in microbial populations [40,46,47]. The subject of cyclic dominance is reviewed in detail in [44]. Interestingly, when finite-size effects are taken into account, cyclic dominance may fail to sustain biodiversity and may even be responsible for extinction [48]. Further results indicate that competition is key for sustaining biodiversity whilst ecosystem-wide patterns form by means of cyclical interactions [49]. Dynamically generated cyclic dominance, apart from sustaining biodiversity, offers alternative ways to sustain cooperators even in the face of large temptation to defect [50]. Considering more than three species in ecosystems, the existence of a phase with global oscillations, especially if the interaction graph contains multiple subloops and local cycles, prompts the conjecture that global oscillations are a general characteristic of realistic food webs [51]. Meanwhile, considering more than three strategies in evolutionary games shows that cyclic dominance emerges as an unexpected escape route from the adverse effects of antisocial punishment, also providing an explanation as to why second-order free-riding may not impede the evolutionary stability of punishment [52]. Here, we considerably expand the scope of cyclic dominance in the generic and broadly adaptable setting of the voluntary social dilemma. Motivated by the ubiquity of risk aversion in the real world, we introduce a fourth player type, hedgers, who are also risk averse, but in a more sophisticated and productive way than loners. Instead of avoiding meaningful interaction altogether, hedgers are willing to pay a hedging cost that allows them to learn the strategy of their opponents and thus avoid getting exploited. Specifically, a hedger enacts tit-for-tat play, but without cooperation in the first move [53–55]. If the opponent defects, the hedger also defects, whereas if the opponent cooperates, the hedger also cooperates.

In the described setting, hedgers may replace loners in a closed loop of dominance such that defectors invade cooperators, but cooperators invade hedgers, and hedgers invade defectors. We thus report a novel route to cyclic dominance in the voluntary social dilemma made possible by risk aversion. Strategy abundances again oscillate in time, but oscillations are now induced by more elaborate and productive means than the simplistic loner strategy [31]. This is possible when the cost of hedging is sufficiently low. When the cost of hedging gets high, loners dominate hedgers, and we recover the original voluntary dilemma. For intermediate hedging costs, other solutions are also stable, including a

Table 1. Bilateral pay-off matrix in the basic prisoner's dilemma game. A way to interpret this matrix is to assume that the pay-off in a particular row and column is earned when a strategy in the first row is met with a strategy in the first column. Thus, pay-off S is earned by a cooperator C meeting a defector D. The pay-off order is $T > R > P > S$ to encourage defection and discourage cooperation. Also, $2R > T + S$ makes mutual cooperation ($2R$) more beneficial for the collective than defecting against a cooperator ($T + S$).

	C	D
C	R	S
D	T	P

four-strategy state in which all competing strategies coexist, or a two-strategy state in which cooperators and defectors coexist as is common in spatial prisoner's dilemmas [56].

We hereafter proceed by detailing the mathematical model, describing the main results, and discussing their broader implications. We envision more direct applications to complex social systems, yet adaptations to biological systems also seem plausible.

2. Mathematical model

Our model is a variant of the prisoner's dilemma game (PDG) extended to incorporate loners and hedgers. In a common PDG [53], mutual cooperation is rewarded by the reward pay-off, R, whereas mutual defection is punished by the punishment pay-off, P. Furthermore, defection is encouraged by the largest pay-off, temptation T, while cooperation is discouraged by the lowest sucker's pay-off, S. This is because of the pay-off ranking $T > R > P > S$, and the fact that T is earned by a defector upon meeting a cooperator who then earns S. In the repeated version of the game, it is additionally assumed that $2R > T + S$ [57]. The corresponding bilateral pay-off matrix is given in table 1. Although the game seems to be defined by four pay-offs, there is a well-known rescaling to two parameters that leaves the evolutionary dynamics unaffected [26]. For even more simplicity, studies often resort to the weak PDG [56], in which only one parameter, $T = b$, controls how strong the dilemma is in the sense that the larger the value of b, the stronger is the temptation to defect. The other pay-offs are simplified to $R = 1$ and $P = S = 0$.

We extended the weak PDG to include loners and hedgers. A loner avoids complications by always earning a small pay-off, $\sigma \ll b$, which is also earned by anyone who meets the loner. A hedger, by contrast, is much more sophisticated. Because of the hedger's risk aversion, they pay a hedging cost, α, to learn the opponent's strategy, and then enact tit-for-tat play by cooperating with a cooperator or defecting against a defector. With the pay-offs of all four strategies defined (table 2), it is worthwhile briefly examining implications for the evolutionary dynamics.

Focusing momentarily on the CDL combination of players [29,30], we see that, in the absence of cooperators, loners receive the same or larger pay-off than defectors, giving the former strategy a decisive evolutionary advantage over the latter. The situation is similar for defectors against cooperators in the absence of loners, and for cooperators against loners in the absence of defectors. Based on these

Table 2. Bilateral pay-off matrix of the four-strategy model. As in table 1, the pay-off in a particular row and column is earned when a strategy in the first row is met with a strategy in the first column. For example, pay-off b is earned by a defector D meeting a cooperator C, whereas pay-off σ is earned by a hedger H meeting a loner L.

	C	D	L	H
C	1	0	σ	1
D	b	0	σ	0
L	σ	σ	σ	σ
H	$1-\alpha$	$-\alpha$	σ	$1-\alpha$

observations, it is a fair guess even before running any simulations that cyclic dominance may emerge, especially when the game is embedded into a spatial structure.

For the *CDH* combination of players, the set-up is somewhat different. The relation between cooperators and defectors in the absence of hedgers remains unchanged, of course, and the relation between cooperators and hedgers mimics that of cooperators and loners because, in the absence of defectors, it is cooperators who always attain a larger pay-off. The relation between defectors and hedgers is complicated by the fact that, in the absence of cooperators, either strategy may earn more depending on who interacts with whom and what the exact value of hedging cost α is. Nonetheless, when the cost is small and hedgers sufficiently abundant, they should be able to overcome defection, possibly giving rise to cyclic dominance once again. We examined this supposition using Monte Carlo simulations [57,58] as well as the pair approximation technique [57,59] (electronic supplementary material). Monte Carlo simulations of evolutionary games are an individual-based approach in which the actions of each individual are implemented explicitly to generate a pay-off that is then compared with the pay-offs of other individuals, followed by imitation of those who performed better. Simulations are typically run until the system reaches a stable state as indicated by an order parameter, e.g. the fraction of cooperators. The pair approximation method provides alternative means of tracking the system's state. Specifically, by focusing on the frequencies and the proportions of strategy pairs, the method yields a set of differential equations that should implicitly encode the behaviours that are explicit in Monte Carlo simulations. As such, pair approximation can be used to verify the results of Monte Carlo simulations or offer a different perspective on particular outcomes.

For the purpose of Monte Carlo simulations, we arranged a total of $N = L^2$ agents to form a square lattice of length L with periodic boundary conditions. Each agent is characterized by a strategy vector, $S_x = (p_x^C, p_x^D, p_x^L, p_x^H)^T$, where p_x^* is the probability with which agent x behaves as a cooperator, defector, loner, or hedger. A direct consequence is that $p_x^C + p_x^D + p_x^L + p_x^H = 1$. We additionally imposed that exactly one p_x^* equals unity, meaning that the only four possible strategy vectors for agent x are $S_x = (1, 0, 0, 0)^T \equiv C$, $S_x = (0, 1, 0, 0)^T \equiv D$, $S_x = (0, 0, 1, 0)^T \equiv L$, and $S_x = (0, 0, 0, 1)^T \equiv H$. Then the pay-off earned by this agent in a single round of the game is

$$P_x = \sum_{y \in \mathrm{N}_x} S_x^T \mathbf{M} S_y, \qquad (2.1)$$

where N_x is the set of agent x's neighbours, $\mathbf{M}$ is the matrix of elementary pay-offs as displayed in table 2, and S_y is the strategy vector of x's neighbour y. Depending on the earned pay-offs, agents update their strategies using the Fermi rule [57,58], which ensures that poorer performing players eventually adopt the strategies of their better performing counterparts. Specifically, agent x imitates the strategy of a randomly chosen neighbour $y \in \mathrm{N}_x$ with probability

$$W_{S_x \leftarrow S_y} = \frac{1}{1 + \exp\left((P_x - P_y)/K\right)}, \qquad (2.2)$$

where K quantifies the irrationality of selection, i.e. the larger the K is, the greater the probability that agent x imitates agent y even if $P_x > P_y$.

To run simulations from this point on, we only needed to specify parameter values. The pay-off parameter whose value was held constant throughout this study is $\sigma = 0.3$. To uphold constraint $2R > T + S$, we examined temptation pay-offs in the range $1 \leq b \leq 2$; $b = 2$ thus signifies the strongest dilemma. Furthermore, we presented the results for hedging costs in the range $0 \leq \alpha \leq 0.4$ because there are no qualitative changes in the system's behaviour for $\alpha > 0.4$. The lattice size systematically varied in the range $200 \leq L \leq 1500$ to make sure that the results are not due to the finite size effects. The closed neighbourhood was von Neumann's [58] throughout the study. Relative to an arbitrarily selected focal agent, such a neighbourhood includes the closest 'north', 'east', 'south' and 'west' agents, implying a constant node degree of $k = 4$. Finally, the irrationality of the selection parameter was kept constant at $K = 0.1$. We ran each simulation over 50 000 time steps to guarantee that the transient dynamics had passed.

3. Results

Simulations reveal that hedgers are able to support cooperation via cyclic dominance. When the hedging cost is sufficiently low, hedgers outlive loners and remain abundant over the whole range of temptation pay-offs (figure 1*a*). In doing so, hedgers enter into a loop of cyclic dominance with cooperators and defectors, helping the former to avoid being overrun by the latter. How this transpires is more clearly seen in the snapshots of evolutionary dynamics in which defectors invade cooperators, who invade hedgers, who invade loners early on (second column in figure 2). Afterwards, however, hedgers maintain their presence by paying little cost while denying defectors the temptation pay-off and enjoying the reward pay-off with cooperators (top row in figure 2). Under such conditions, loners are the least competitive player type whose eventual disappearance marks the beginning of cyclic dominance between cooperators, defectors, and hedgers. That these player types indeed cyclically dominate one another is reflected in the irregular mixing pattern of agents post transient evolutionary dynamics (fifth column in figure 2).

Loners start replacing hedgers as the hedging cost increases. This first happens for small (figure 1*b*) and then all (figure 1*c*) values of the temptation pay-off. Despite losing the support from hedgers, cooperators do not succumb to defectors because it is now loners who enter the loop of cyclic dominance. The snapshots of evolutionary dynamics illustrate this turn of events. As hedgers become overburdened by their risk-averse strategy due to the high hedging
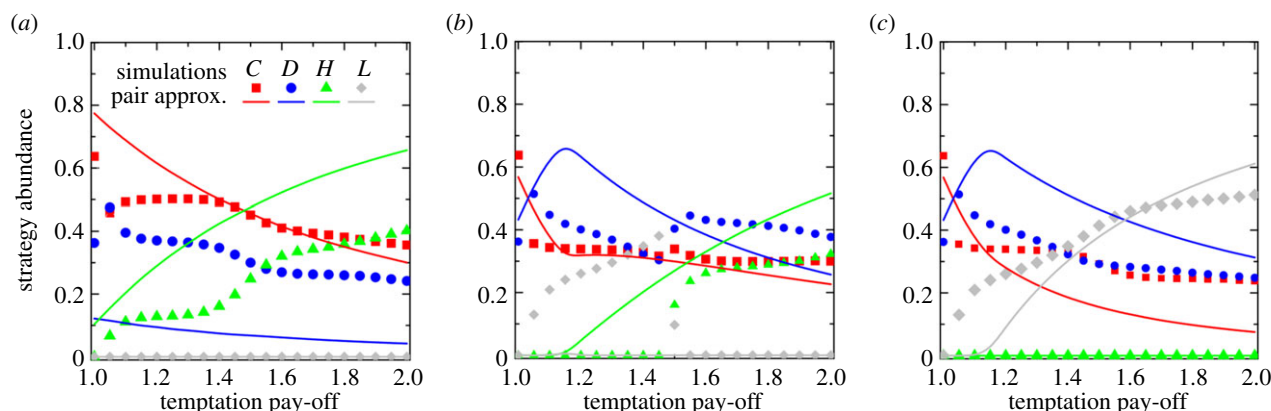
Figure 1. Hedgers and loners interchangeably support cooperation via cyclic dominance. (a) When hedging costs are low, $\alpha = 0.05$, hedgers are more competitive than loners and manage to support cooperation via cyclic dominance over the full range of temptation pay-offs. (b) When hedging costs are intermediate, $\alpha = 0.22$, hedgers are more competitive than loners only over a limited range of temptation pay-offs. Cooperation is, nonetheless, supported via cyclic dominance as loners assume an analogous role to hedgers while the temptation pay-off stays relatively low. (c) With high hedging costs, $\alpha = 0.4$, hedgers are no longer competitive at all. Cooperation is then maintained via cyclic dominance solely by loners. Simulation and pair-approximation results differ quantitatively, but they tell the same story qualitatively.
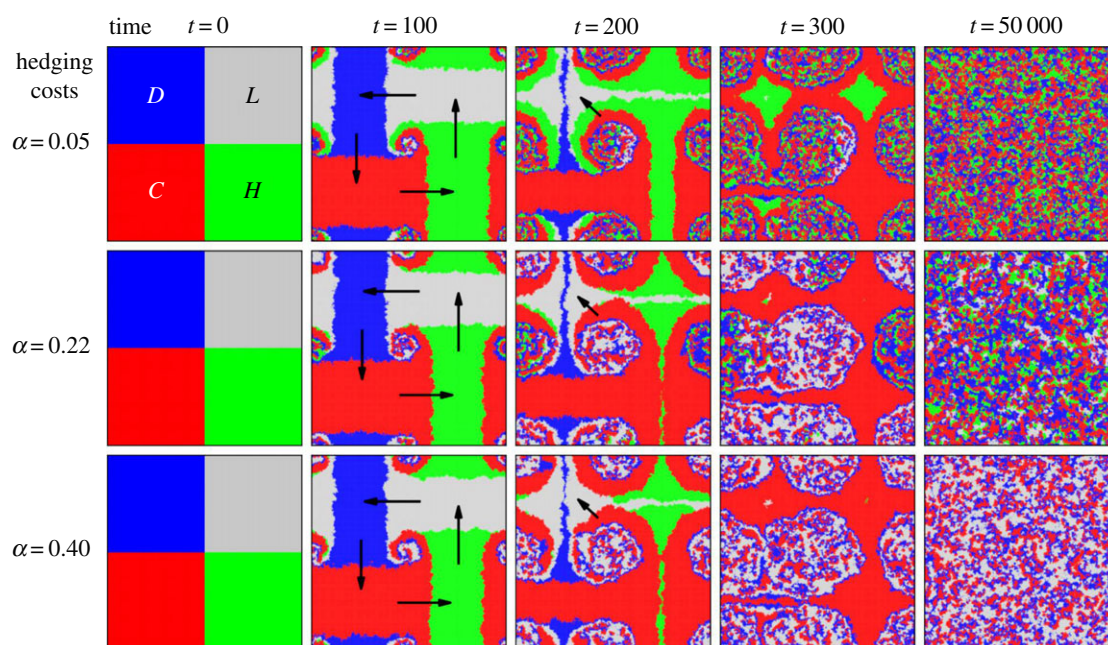

Figure 2. Hedging costs shape the fate of hedgers. Shown are the snapshots of evolutionary dynamics at different time steps (columns) and for different hedging costs (rows). Early in the evolutionary dynamics, defectors invade cooperators, who invade hedgers, who invade loners. Later, however, it is hedging costs that determine the fate of hedgers. When these costs are low (top row), hedgers pay little for denying defectors the temptation pay-off, as well as enjoying the reward pay-off together with cooperators. All this helps hedgers to outlive loners, who eventually disappear. When hedging costs are high (bottom row), risk aversion is a burden that cannot be offset by the reward pay-off. Hedgers eventually disappear. Finally, when hedging costs are intermediate (middle row), there is a balance of power of sorts between hedgers and loners, and all four strategies survive. The irregular mixing of strategies after transient evolutionary dynamics is a signature of cyclic dominance.

cost, they become the least competitive player type and eventually die out (bottom row in figure 2). The recognizable irregular mixing pattern of agents engaged in cyclic dominance resurfaces again after transient evolutionary dynamics, but now with loners having taken the place of hedgers. Interestingly, although hedgers and loners almost entirely exclude one another, there is a narrow window of hedging costs and temptation pay-offs in which these two player types coexist alongside cooperators and defectors (middle row in figure 2).

To have a glimpse into the heart of cyclic dominance, we estimated invasion rates post transient evolutionary

dynamics. If strategy S_x had been invaded by strategy S_y, we defined the corresponding invasion rate, $w_{S_x \leftarrow S_y} > 0$, as the net positive fraction of transitions from strategy S_x to strategy S_y mediated by the Fermi rule in a single Monte Carlo time step. With four player types, six invasions had been possible. These happened to be $w_{C \leftarrow D}$, $w_{L \leftarrow C}$, $w_{H \leftarrow C}$, $w_{D \leftarrow L}$, $w_{D \leftarrow H}$, and $w_{L \leftarrow H}$.

Invasion rates clearly demonstrate cyclic dominance in action. For an intermediate temptation pay-off, $b = 1.5$, and relatively low hedging costs, cooperators, defectors, and hedgers get locked in a cyclic dominance loop as evidenced by the equality of invasion rates $w_{C \leftarrow D} = w_{D \leftarrow H} = w_{H \leftarrow C}$
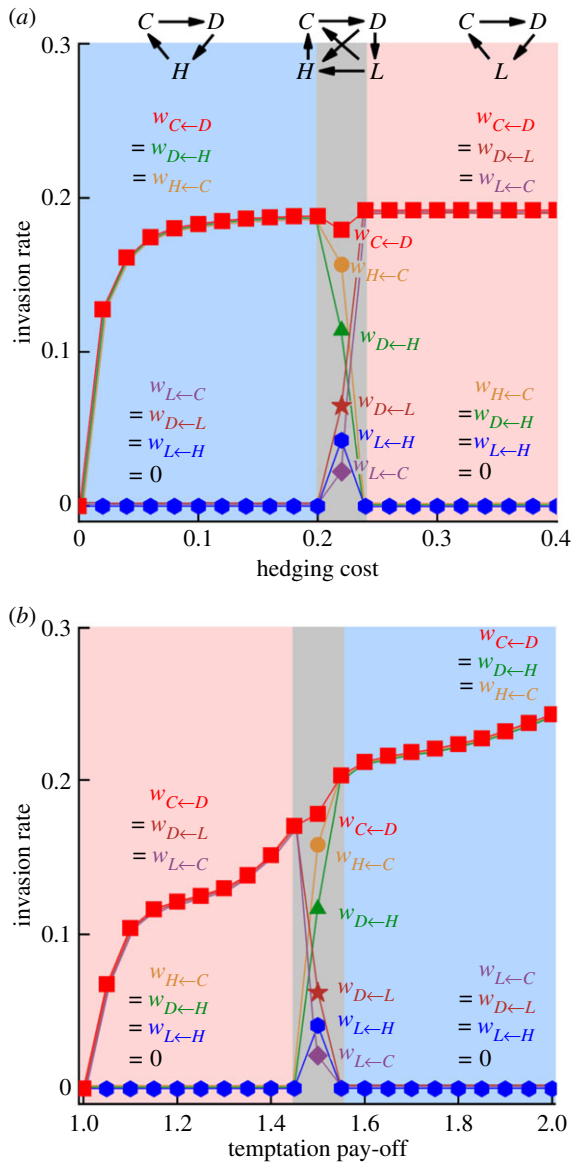
Figure 3. Average invasion rates reveal cyclic dominance in action. (*a*) Fixing the temptation pay-off to $b = 1.5$, we plotted average invasion rates as the functions of hedging costs, α. For small α values, cyclic dominance between cooperators, defectors, and hedgers (light-blue area) is reflected in the fact that defectors invade cooperators, who invade hedgers, who invade defectors all with the same average invasion rate. For large α values, the situation is analogous, except that loners take the place of hedgers (light-red area). For a narrow window of intermediate α values, the two cyclic dominance loops intermix, with hedgers actually invading loners with a small invasion rate ($w_{L \leftarrow H}$) that is more than compensated for by loners invading defectors ($w_{D \leftarrow L} > w_{L \leftarrow H}$), which enables all four strategies to coexist. (*b*) Similar results are obtained by fixing the hedging cost to an intermediate value of $\alpha = 0.22$, and then varying the temptation benefit. Here, cyclic dominance with loners emerges for small b values (light-red area), whereas cyclic dominance with hedgers emerges for large b values (light-blue area).
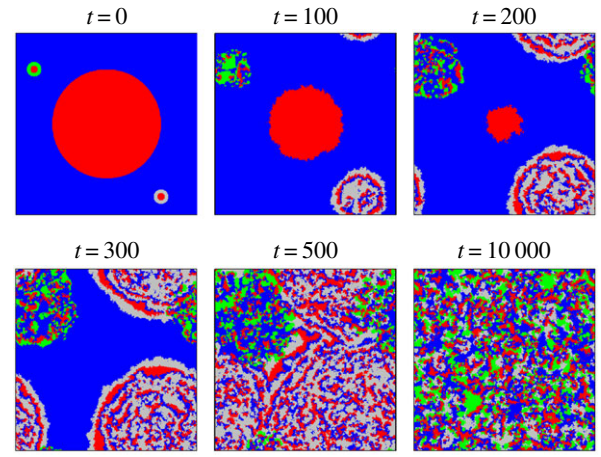

Figure 4. Hedgers and loners protect cooperators even in the harshest of conditions. Shown is the time evolution of strategies such that, initially, there is a one giant cluster of cooperators (red) surrounded by defectors (blue), and two smaller clusters of cooperators separated from defectors by a thin layer of hedgers (green) in one case and loners (grey) in the other. The temptation pay-off, $b = 2.0$, is at the maximum of the prisoner's dilemma limits. The hedging cost of $\alpha = 0.26$ is intermediate. Under such conditions, the giant cooperative cluster quickly erodes under exploitation by defectors. Smaller cooperative clusters, by contrast, turn into mixes of cooperators, defectors, and loners or hedgers, that spread like ripples across a lattice; here, of size $L = 500$.

(figure 3*a*). All invasion rates involving loners equal zero because players of this type get outcompeted. As hedging costs increase, the fortunes of hedgers and loners reverse, and now the latter get locked in the cyclic dominance loop with cooperators and defectors as indicated by equalities $w_{C \leftarrow D} = w_{D \leftarrow L} = w_{L \leftarrow C}$ (figure 3*a*). All invasion rates involving hedgers equal zero because hedgers get outcompeted, just as loners did in the opposite situation. All four

player types coexists only over a narrow window of intermediate hedging costs. Here, cooperators are drained in favour of defectors, but replenished at the expense of hedgers and loners, i.e. $w_{C \leftarrow D} = w_{H \leftarrow C} + w_{L \leftarrow C}$. Defectors are drained in favour of hedgers and loners, but replenished at the expense of cooperators, i.e. $w_{D \leftarrow H} + w_{D \leftarrow L} = w_{C \leftarrow D}$. Loners are drained in favour of hedgers and cooperators, but replenished at the expense of defectors, i.e. $w_{L \leftarrow H} + w_{L \leftarrow C} = w_{D \leftarrow L}$. Finally, hedgers are drained in favour of cooperators, but replenished at the expense of defectors and loners, i.e. $w_{H \leftarrow C} = w_{D \leftarrow H} + w_{L \leftarrow H}$. Completely analogous results hold when the hedging cost is intermediate, $\alpha = 0.22$, and the temptation pay-off increases in the range $1 \leq b \leq 2$ (figure 3*b*).

Cyclic dominance emerges rather independently of the initial conditions and even in the face of the strongest dilemma, $b = 2.0$. To demonstrate this, we present simulations of the evolutionary dynamics starting from one large cluster of cooperators surrounded entirely by defectors, and two small clusters of cooperators, but separated from defectors by a thin layer of hedgers in one case and loners in the other (figure 4). Setting the hedging cost to an intermediate value, $\alpha = 0.32$, we find that defectors quickly chip away at the large cooperative cluster, while smaller cooperative clusters turn into a mix of cooperators, defectors, and hedgers or loners, and spread in a ripple-like manner through the lattice, until cyclic dominance becomes omnipresent (figure 4).

To fully understand evolutionary dynamics as a function of the temptation pay-off and the hedging cost, we mapped the system's phase space. We found four distinct phases: cooperators and defectors only ($C + D$), cooperators–defectors–hedgers ($C + D + H$), cooperators–defectors–loners ($C + D + L$), and all four player types ($C + D + L + H$). When the temptation benefit is very small, the dilemma is minimal and the system evolves to the $C + D$ phase irrespective of the hedging cost (figure 5*a*). As the temptation pay-off increases, it is the hedging
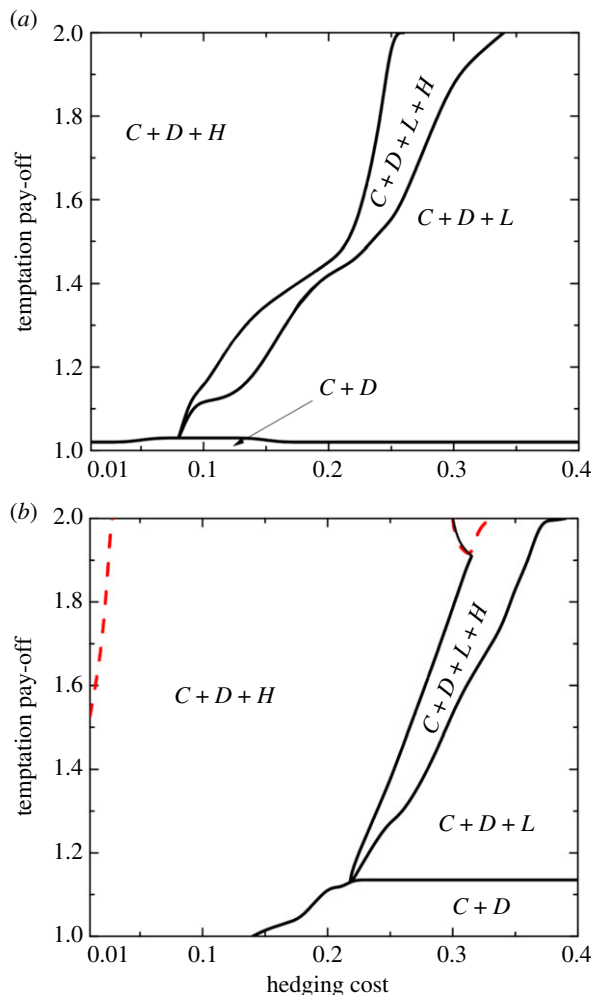
Figure 5. Cyclic dominance is a widespread phenomenon. Shown are the phase diagrams due to Monte Carlo simulations and the pair approximation, revealing the model's dynamical regimes as a function of the hedging cost and the temptation pay-off. (a) Cyclic dominance arises almost everywhere in the phase space of Monte Carlo simulations, with hedgers surviving at low and loners at high hedging costs. There is also a narrow domain in which all four strategies coexist. (b) Pair approximation yields a qualitatively similar distribution of strategy prevalences. Dashed red curves delineate subdomains where the system converges to limit cycles by which the abundances of surviving player types oscillate in time (figure 6).

cost that largely determines how the system evolves. For relatively small hedging costs the $C+D+H$ phase is prevalent, whereas for relatively large hedging costs the $C+D+L$ phase is prevalent (figure 5a). There is only a narrow window of intermediate hedging costs in which the system evolves to the $C+D+L+H$ phase (figure 5a), showing again that hedgers and loners almost interchangeably support cooperation through cyclic dominance. The pair approximation yields a qualitatively similar phase diagram, despite some obvious quantitative differences relative to Monte Carlo simulations (figure 5b).

It is not entirely equivalent whether cyclic dominance is established by hedgers or loners. Namely, in the spatial voluntary dilemma, cyclic dominance gives rise to oscillating strategy abundances everywhere on the b–α phase diagram, but without spatial structure only cyclic dominance involving hedgers can do so indefinitely. Fixing the temptation pay-off to $b = 2.0$ and choosing a low hedging cost of $\alpha = 0.02$ places the system in the $C+D+H$ phase such that the pair

approximation generates an open cycle trajectory that converges to a planar limit cycle (figure 6a). The limit cycle is planar because loners die out and the sum of strategy abundances for the remaining three player types is constrained to unity. Increasing the cost of hedging to a higher value of $\alpha = 0.32$ sets the system into the $C+D+L+H$ phase in which evolutionary dynamics converges to a three-dimensional limit cycle (figure 6b) because now all four player types coexist, but their abundances are still constrained to unity. Finally, with a high hedging cost of $\alpha = 0.4$, the system is pushed into the $C+D+L$ phase, where the pair approximation yields a trajectory with small open cycles that disappear as the system converges to a stable equilibrium with zero hedgers (figure 6c). A degree of cooperation is still maintained in such an equilibrium, but cyclic dominance as the underlying cause stays masked by the static outcome of evolutionary dynamics.

4. Discussion

Herein, we revealed a novel route to cyclic dominance in voluntary social dilemmas brought about by risk-averse players called hedgers. These players outwit defectors by paying a hedging cost to avoid getting exploited. In the presence of cooperators, however, risk aversion is redundant and thus a burden that hampers performance. Hedgers accordingly invade defectors, defectors—as usual in social dilemmas—invade cooperators, and cooperators invade hedgers to close the loop of cyclic dominance. This effectively sustains cooperation even under adverse conditions, when the temptation to defect is high. Moreover, this shows that cooperativeness by way of cyclic dominance can emerge due to more elaborate and productive means than the exceedingly simple loner strategy.

Hedgers may superficially resemble a simple hybrid of cooperators and defectors, yet as risk-averse conditional cooperators they are much more. Plain conditional cooperators, because of their relationship to the tit-for-tat strategy [60], have played a central role in the studies on the evolution of cooperation [61–63]. Adding to this the fact that risk aversion is ubiquitous in real life [64], the importance of considering risk-averse conditional cooperators can hardly be overstated.

Our research has important implications for promoting and sustaining cooperation in human societies. An increasing realism via higher strategic complexity [65–67] is necessarily accompanied by an increasing complexity of evolutionary outcomes as they become dependent not just on individual strategic relations prescribed by pay-off elements, but also on dynamical relations and spontaneously emerging alliances between strategy subsets [44]. Cyclic dominance with hedgers is one such example, but we expect to see many more in the near future. This, in turn, predicts considerable challenges in steering complex social systems towards a desired cooperative state. Simple interventions, as frequently enacted by decision makers, often turn out to be naive and risky propositions precisely because of a limited understanding of the underlying spatio-temporal dynamics that govern social complexity. Relevant examples include producing and appointing inadequately trained personnel [68], flawed models and agency costs associated with those models [69], misunderstanding or ignoring systemic risks [70], etc.

Aside from applications to social dynamics, it is possible to envision analogous, if more complicated, set-ups in
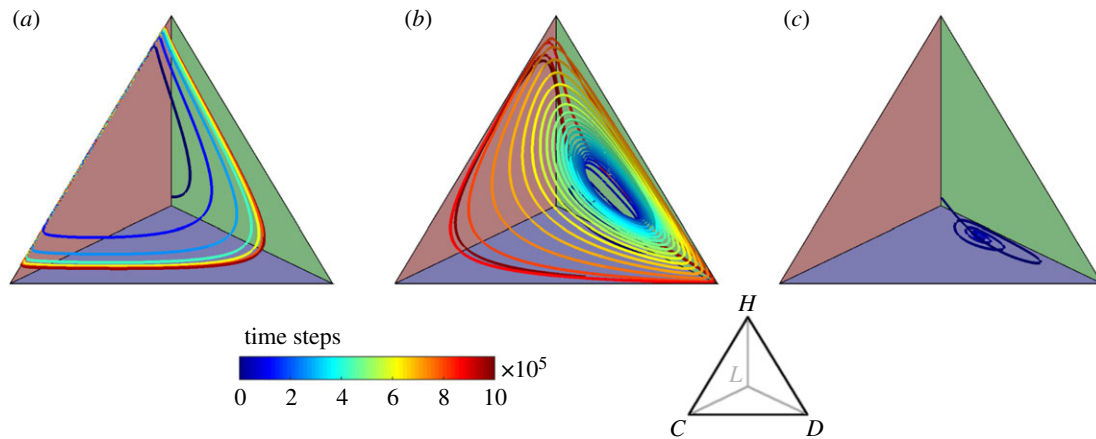
Figure 6. Exceeding simplicity of the loner strategy is manifest in the absence of an explicit spatial structure. Specifically, when approximating the system using pair approximation, hedgers can still maintain cyclic dominance such that strategy abundances oscillate in time, but loners cannot. (*a*) With low hedging costs, $\alpha = 0.02$, and a sufficiently large temptation pay-off, $b = 2.0$, loners quickly disappear as the system converges to a planar limit cycle with positive cooperator, defector, and hedger abundances. The limit cycle is planar because the three strategy abundances must sum to unity. (*b*) When the hedging cost increases to $\alpha = 0.32$, all four strategies coexist and the system converges to a three-dimensional limit cycle. The limit cycle is three dimensional because strategy abundances must again sum to unity. (*c*) With high hedging costs, $\alpha = 0.40$, it is hedgers, and with them oscillations in strategy abundances, who quickly disappear. The system thus approaches a stable equilibrium of cooperator, defector and loner strategies. The colour bar indicates time steps.

biological systems as well. Living tissues are genetically identical cell structures of the same differentiation fate that work cooperatively to support homeostasis [71]. Such cooperative cell structures are susceptible to cheating [71], i.e. individual cells occasionally defect and turn malignant by either increasing their own fitness or decreasing the fitness of the surrounding cells [72–74]. The system is, furthermore, policed by free-ranging immune cells that scan for malignant activity [75,76] and actively punish defectors at a cost [77,78], while receiving compensation for that cost through interactions with cooperative cells. In this sense, cooperative cells would not 'invade', but rather 'modulate', the activity of immune cells, yet the resulting dynamics should still resemble cyclic dominance. Understanding such dynamics by, for example, mapping the system's phase space could help to devise novel treatments for controlling malignant activity [76,79].

While there is a potential for widespread uses, we hope that our research will, at the very least, lead to better understanding of cooperation in social dilemmas. In this context, a particularly promising way forward is to pair up theoretical treatises of evolutionary game dynamics with laboratory [80,81] and even field experiments. Doing so should put the theory to the test, help to identify more solid fundamentals on which to build and overall strongly aid the quest for a better and more sustainable future.

References

1. Vasconcelos VV, Santos FC, Pacheco JM. 2013 A bottom-up institutional approach to cooperative governance of risky commons. *Nat. Clim. Change* **3**, 797–801. (doi:10.1038/nclimate1927)

2. Pacheco JM, Vasconcelos VV, Santos FC. 2014 Climate change governance, cooperation and self-organization. *Phys. Life Rev.* **11**, 573–586. (doi:10.1016/j.plrev.2014.02.003)

3. Hardin G. 1968 The tragedy of the commons. *Science* **162**, 1243–1248. (doi:10.1126/science.162.3859.1243)

4. Ciriacy-Wantrup SV, Bishop RC. 1975 Common property as a concept in natural resources policy. *Nat. Res. J.* **15**, 713–727.

5. Bringezu S, Potočnik J, Schandl H, Lu Y, Ramaswami A, Swilling M, Suh S. 2016 Multi-scale governance of sustainable natural resource use—challenges and opportunities for monitoring and institutional development at the national and global level. *Sustainability* **8**, 778. (doi:10.3390/su8080778)

6. Wu B, Fu F, Wang L. 2011 Imperfect vaccine aggravates the long-standing dilemma of voluntary vaccination. *PLoS ONE* **6**, e20577. (doi:10.1371/journal.pone.0020577)

7. Chen X, Fu F. 2019 Imperfect vaccine and hysteresis. *Proc. R. Soc. B* **286**, 20182406. (doi:10.1098/rspb.2018.2406)

8. Wang Z, Bauch CT, Bhattacharyya S, d'Onofrio A, Manfredi P, Perc M, Perra N, Salathé M, Zhao D. 2016 Statistical physics of vaccination. *Phys. Rep.* **664**, 1–113. (doi:10.1016/j.physrep.2016.10.006)

9. Kuga K, Tanimoto J, Jusup M. 2019 To vaccinate or not to vaccinate: a comprehensive study of vaccination-subsidizing policies with multi-agent simulations and mean-field modeling. *J. Theor. Biol.* **469**, 107–126. (doi:10.1016/j.jtbi.2019.02.013)

10. Chen X, Fu F. 2018 Social learning of prescribing behavior can promote population optimum of antibiotic use. *Front. Phys.* **6**, 193. (doi:10.3389/fphy.2018.00139)

11. D'Orsogna MR, Perc M. 2015 Statistical physics of crime: a review. *Phys. Life Rev.* **12**, 1–21. (doi:10.1016/j.plrev.2014.11.001)

12. Helbing D et al. 2015 Saving human lives: what complexity science and information systems can contribute. *J. Stat. Phys.* **158**, 735–781. (doi:10.1007/s10955-014-1024-9)

13. Pastor-Satorras R, Castellano C, Van Mieghem P, Vespignani A. 2015 epidemic processes in complex networks. *Rev. Mod. Phys.* **87**, 925. (doi:10.1103/RevModPhys.87.925)

14. West SA, Griffin AS, Gardner A. 2007 Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *J. Evol. Biol.* **20**, 415–432. (doi:10.1111/j.1420-9101.2006.01258.x)

15. Pennisi E. 2005 How did cooperative behavior evolve. *Science* **309**, 93. (doi:10.1126/science.309.5731.93)

16. Nowak MA. 2006 Five rules for the evolution of cooperation. *Science* **314**, 1560–1563. (doi:10.1126/science.1133755)

17. Rand DG, Nowak MA. 2013 Human cooperation. *Trends Cogn. Sci.* **17**, 413–425. (doi:10.1016/j.tics.2013.06.003)

18. Kraft-Todd G, Yoeli E, Bhanot S, Rand D. 2015 Promoting cooperation in the field. *Curr. Opin. Behav. Sci.* **3**, 96–101. (doi:10.1016/j.cobeha.2015.02.006)

19. Perc M, Jordan JJ, Rand DG, Wang Z, Boccaletti S, Szolnoki A. 2017 Statistical physics of human cooperation. *Phys. Rep.* **687**, 1–51. (doi:10.1016/j.physrep.2017.05.004)

20. Capraro V, Perc M. 2018 Grand challenges in social physics: in pursuit of moral behavior. *Front. Phys.* **6**, 107. (doi:10.3389/fphy.2018.00107)

21. West SA, Griffin AS, Gardner A. 2007 Evolutionary explanations for cooperation. *Curr. Biol.* **17**, R661–R672. (doi:10.1016/j.cub.2007.06.004)

22. Hofbauer J, Sigmund K. 1998 *Evolutionary games and population dynamics*. Cambridge, UK: Cambridge University Press.

23. Nowak MA. 2006 *Evolutionary dynamics*. Cambridge, MA: Harvard University Press.

24. Sigmund K. 2010 *The calculus of selfishness*. Princeton, NJ: Princeton University Press.

25. Santos FC, Pacheco JM, Lenaerts T. 2006 Evolutionary dynamics of social dilemmas in structured heterogeneous populations. *Proc. Natl Acad. Sci. USA* **103**, 3490–3494. (doi:10.1073/pnas.0508201103)

26. Wang Z, Kokubo S, Jusup M, Tanimoto J. 2015 Universal scaling for the dilemma strength in evolutionary games. *Phys. Life Rev.* **14**, 1–30. (doi:10.1016/j.plrev.2015.04.033)

27. Allen B, Lippner G, Chen Y-T, Fotouhi B, Nowak MA, Yau S-T. 2017 Evolutionary dynamics on any population structure. *Nature* **544**, 227–230. (doi:10.1038/nature21723)

28. Fotouhi B, Momeni N, Allen B, Nowak MA. 2019 Evolution of cooperation on large networks with community structure. *J. R. Soc. Interface* **16**, 20180677. (doi:10.1098/rsif.2018.0677)

29. Szabó G, Hauert C. 2002 Evolutionary prisoner's dilemma games with voluntary participation. *Phys. Rev. E* **66**, 062903. (doi:10.1103/PhysRevE.66.062903)

30. Wu Z-X, Xu X-J, Chen Y, Wang Y-H. 2005 Spatial prisoner's dilemma game with volunteering in Newman-Watts small-world networks. *Phys. Rev. E* **71**, 037103. (doi:10.1103/PhysRevE.71.037103)

31. Semmann D, Krambeck H-J, Milinski M. 2003 Volunteering leads to rock-paper-scissors dynamics in a public goods game. *Nature* **425**, 390–393. (doi:10.1038/nature01986)

32. Szolnoki A, Perc M. 2013 Correlation of positive and negative reciprocity fails to confer an evolutionary advantage: phase transitions to elementary strategies. *Phys. Rev. X* **3**, 041021. (doi:10.1103/physrevx.3.041021)

33. Szolnoki A, Perc M, Szabó G. 2012 Defense mechanisms of empathetic players in the spatial ultimatum game. *Phys. Rev. Lett.* **109**, 078701. (doi:10.1103/PhysRevLett.109.078701)

34. Requejo RJ, Camacho J, Cuesta JA, Arenas A. 2012 Stability and robustness analysis of cooperation cycles driven by destructive agents in finite populations. *Phys. Rev. E* **86**, 026105. (doi:10.1103/PhysRevE.86.026105)

35. Szolnoki A, Perc M. 2009 Resolving social dilemmas on evolving random networks. *EPL* **86**, 30007. (doi:10.1209/0295-5075/86/30007)

36. Perc M, Szolnoki A. 2010 Coevolutionary games—a mini review. *BioSystems* **99**, 109–125. (doi:10.1016/j.biosystems.2009.10.003)

37. Frachebourg L, Krapivsky PL, Ben-Naim E. 1996 Segregation in a one-dimensional model of interacting species. *Phys. Rev. Lett.* **77**, 2125. (doi:10.1103/PhysRevLett.77.2125)

38. Frean M, Abraham ED. 2001 Rock–scissors–paper and the survival of the weakest. *Proc. R. Soc. B* **268**, 1323–1327. (doi:10.1098/rspb.2001.1670)

39. Kerr B, Riley MA, Feldman MW, Bohannan BJM. 2002 Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. *Nature* **418**, 171–174. (doi:10.1038/nature00823)

40. Kirkup BC, Riley MA. 2004 Antibiotic-mediated antagonism leads to a bacterial game of rock-paper-scissors in vivo. *Nature* **428**, 412–414. (doi:10.1038/nature02429)

41. Mobilia M, Georgiev IT, Täuber UC. 2006 Fluctuations and correlations in lattice models for predator-prey interaction. *Phys. Rev. E* **73**, 040903(R). (doi:10.1103/PhysRevE.73.040903)

42. Reichenbach T, Mobilia M, Frey E. 2007 Mobility promotes and jeopardizes biodiversity in rock-paper-scissors games. *Nature* **448**, 1046–1049. (doi:10.1038/nature06095)

43. Mobilia M. 2010 Oscillatory dynamics in rock-paper-scissors games with mutations. *J. Theor. Biol.* **264**, 1–10. (doi:10.1016/j.jtbi.2010.01.008)

44. Szolnoki A, Mobilia M, Jiang L-L, Szczesny B, Rucklidge AM, Perc M. 2014 Cyclic dominance in evolutionary games: a review. *J. R. Soc. Interface* **11**, 20140735. (doi:10.1098/rsif.2014.0735)

45. Kelsic ED, Zhao J, Vetsigian K, Kishony R. 2015 Counteraction of antibiotic production and degradation stabilizes microbial communities. *Nature* **521**, 516–519. (doi:10.1038/nature14485)

46. Durrett R, Levin S. 1997 Allelopathy in spatial distributed populations. *J. Theor. Biol.* **185**, 165–171. (doi:10.1006/jtbi.1996.0292)

47. Nahum JR, Harding BN, Kerr B. 2011 Evolution of restraint in a structured rock-paper-scissors community. *Proc. Natl Acad. Sci. USA* **108**, 10 831–10 838. (doi:10.1073/pnas.1100296108)

48. Reichenbach T, Mobilia M, Frey E. 2006 Coexistence versus extinction in the stochastic cyclic Lotka-Volterra model. *Phys. Rev. E* **74**, 051907. (doi:10.1103/PhysRevE.74.051907)

49. Jiang L-L, Zhou T, Perc M, Wang B-H. 2011 Effects of competition on pattern formation in the rock-paper-scissors game. *Phys. Rev. E* **84**, 021912. (doi:10.1103/PhysRevE.84.021912)

50. Szolnoki A, Wang Z, Wang J, Zhu X. 2010 Dynamically generated cyclic dominance in spatial prisoner's dilemma games. *Phys. Rev. E* **82**, 036110. (doi:10.1103/PhysRevE.82.036110)

51. Rulquin C, Arenzon JJ. 2014 Globally synchronized oscillations in complex cyclic games. *Phys. Rev. E* **89**, 032133. (doi:10.1103/PhysRevE.89.032133)

52. Szolnoki A, Perc M. 2017 Second-order free-riding on antisocial punishment restores the effectiveness of prosocial punishment. *Phys. Rev. X* **7**, 041027. (doi:10.1103/physrevx.7.041027)

53. Axelrod R. 1984 *The evolution of cooperation*. New York, NY: Basic Books.

54. Nowak MA, Sigmund K. 1993 A strategy of win-stay, lose-shift that outperforms tit-for-tat in the prisoner's dilemma game. *Nature* **364**, 56–58. (doi:10.1038/364056a0)

55. Szolnoki A, Perc M, Szabó G. 2009 Phase diagrams for three-strategy evolutionary prisoner's dilemma games on regular graphs. *Phys. Rev. E* **80**, 056104. (doi:10.1103/PhysRevE.80.056104)

56. Nowak MA, May RM. 1992 Evolutionary games and spatial chaos. *Nature* **359**, 826–829. (doi:10.1038/359826a0)

57. Szabó G, Fáth G. 2007 Evolutionary games on graphs. *Phys. Rep.* **446**, 97–216. (doi:10.1016/j.physrep.2007.04.004)

58. Hauert C. 2002 Effects of space in 2 × 2 games. *Int. J. Bifurc. Chaos* **12**, 1531–1548. (doi:10.1142/S0218127402005273)

59. Hauert C, Szabó G. 2005 Game theory and physics. *Am. J. Phys.* **73**, 405. (doi:10.1119/1.1848514)

60. Fehr E, Fischbacher U. 2004 Social norms and human cooperation. *Trends Cogn. Sci.* **8**, 185. (doi:10.1016/j.tics.2004.02.007)

61. Frey BS, Meier S. 2004 Social comparisons and pro-social behavior: testing 'conditional cooperation' in a field experiment. *Am. Econ. Rev.* **94**, 1717–1722. (doi:10.1257/0002828043052187)

62. Rustagi D, Engel S, Kosfeld M. 2010 Conditional cooperation and costly monitoring explain success in forest commons management. *Science* **330**, 961–965. (doi:10.1126/science.1193649)

63. Suzuki S, Niki K, Fujisaki S, Akiyama E. 2010 Neural basis of conditional cooperation. *Soc. Cogn. Affect. Neurosci.* **6**, 338–347. (doi:10.1093/scan/nsq042)

64. Halek M, Eisenhauer JG. 2001 Demography of risk aversion. *J. Risk Insur.* **68**, 1–24. (doi:10.2307/2678130)

65. Capraro V, Cococcioni G. 2015 Social setting, intuition and experience in laboratory experiments interact to shape cooperative decision-making. *Proc. R. Soc. B* **282**, 20150237. (doi:10.1098/rspb.2015.0237)

66. Hauser OP, Rand DG, Peysakhovich A, Nowak MA. 2014 Cooperating with the future. *Nature* **511**, 220–223. (doi:10.1038/nature13530)

67. Jordan JJ, Hoffman M, Bloom P, Rand DG. 2016 Third-party punishment as a costly signal of trustworthiness. *Nature* **530**, 473–475. (doi:10.1038/nature16981)

68. Jacobson SK, McDuff MD. 1998 Training idiot savants: the lack of human dimensions in conservation biology. *Conserv. Biol.* **12**, 263. (doi:10.1046/j.1523-1739.1998.97235.x)

69. Gerding EF. 2009 Code, crash, and open source: the outsourcing of financial regulation to risk models and the global financial crisis. *Wash. L. Rev.* **84**, 127.

70. Haldane AG, May RM. 2011 Systemic risk in banking ecosystems. *Nature* **469**, 351–355. (doi:10.1038/nature09659)

71. Celiker H, Gore J. 2013 Cellular cooperation: insights from microbes. *Trends Cell Biol.* **23**, 9–15. (doi:10.1016/j.tcb.2012.08.010)

72. Merlo LM, Pepper JW, Reid BJ, Maley CC. 2006 Cancer as an evolutionary and ecological process. *Nat. Rev. Cancer* **6**, 924–935. (doi:10.1038/nrc2013)

73. Bozic I *et al*. 2010 Accumulation of driver and passenger mutations during tumor progression. *Proc. Natl Acad. Sci. USA* **107**, 18 545–18 550. (doi:10.1073/pnas.1010978107)

74. Greaves M, Maley CC. 2012 Clonal evolution in cancer. *Nature* **481**, 306–313. (doi:10.1038/nature10762)

75. Reiche EMV, Nunes SOV, Morimoto HK. 2004 Stress, depression, the immune system, and cancer. *Lancet Oncol.* **5**, 617–625. (doi:10.1046/j.1523-1739.1998.97235.x)

76. Finn O. 2012 Immuno-oncology: understanding the function and dysfunction of the immune system in cancer. *Ann. Oncol.* **23**, viii6–viii9. (doi:10.1093/annonc/mds256)

77. Derting TL, Compton S. 2003 Immune response, not immune maintenance, is energetically costly in wild white-footed mice (*Peromyscus leucopus*). *Physiol. Biochem. Zool.* **76**, 744–752. (doi:10.1086/375662)

78. Hanssen SA, Hasselquist D, Folstad I, Erikstad KE. 2004 Costs of immunity: immune responsiveness reduces survival in a vertebrate. *Proc. R. Soc. B* **271**, 925–930. (doi:10.1098/rspb.2004.2678)

79. Couzin-Frankel J. 2013 Cancer immunotherapy. *Science* **342**, 1432–1433. (doi:10.1126/science.342.6165.1432)

80. Rand DG. 2012 The promise of mechanical turk: how online labor markets can help theorists run behavioral experiments. *J. Theor. Biol.* **299**, 172–179. (doi:10.1016/j.jtbi.2011.03.004)

81. Wang Z, Jusup M, Wang R-W, Shi L, Iwasa Y, Moreno Y, Kurths J. 2017 Onymity promotes cooperation in social dilemma experiments. *Sci. Adv.* **3**, e1601444. (doi:10.1126/sciadv.1601444)