

Original Article

Sustained cooperation by running away from bad behavior

Charles Efferson^{a,*}, Carlos P. Roca^{b,*}, Sonja Vogt^a, Dirk Helbing^{c,d,*}^a Department of Economics, University of Zurich^b Department of Chemical Engineering, Universitat Rovira i Virgili, Spain^c Chair of Sociology, In Particular of Modeling & Simulation, Swiss Federal Institute of Technology, Zurich^d Santa Fe Institute, USA

ARTICLE INFO

Article history:

Initial receipt 11 November 2014

Final revision received 15 May 2015

Keywords:

Evolution of cooperation

Positive assortment

Migration

Behavioral experiment

ABSTRACT

For cooperation to evolve, some mechanism must limit the rate at which cooperators are exposed to defectors. Only then can the advantages of mutual cooperation outweigh the costs of being exploited. Although researchers widely agree on this, they disagree intensely about which evolutionary mechanisms can explain the extraordinary cooperation exhibited by humans. Much of the controversy follows from disagreements about the informational regularity that allows cooperators to avoid defectors. Reliable information can allow cooperative individuals to avoid exploitation, but which mechanisms can sustain such a situation is a matter of considerable dispute. We conducted a behavioral experiment to see if cooperators could avoid defectors when provided with limited amounts of explicit information. We gave each participant the simple option to move away from her current neighborhood at any time. Participants were not identifiable as individuals, and they could not track each other's tendency to behave more or less cooperatively. More broadly, a participant had no information about the behavior she was likely to encounter if she moved, and so information about the risk of exploitation was extremely limited. Nonetheless, our results show that simply providing the option to move allowed cooperation to persist for a long period of time. Our results further show that movement, even though it involved considerable uncertainty, allowed would-be cooperators to assort positively and eliminate on average any individual payoff disadvantage associated with cooperation. This suggests that choosing to move, even under limited information, can completely reorganize the mix of selective forces relevant for the evolution of cooperation.

© 2016 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

Paradoxically, the evolution of human cooperation is an area of research characterized by both widespread agreement and seemingly interminable controversy. Regarding the widespread agreement, researchers generally accept that the evolution of cooperation requires some kind of informational regularity (Frank, 1998; Henrich, 2004; Nowak, 2006; van Veelen, 2009; Bowles & Gintis, 2011). In its most general form, this regularity can be thought of as a situation in which a cooperating individual is more likely than a defecting individual to interact with someone who cooperates. Such a regularity means that individuals who cooperate enjoy, with a relatively high probability, the benefits produced when others cooperate. This limits the risk of exploitation and produces mutual gains that can support the evolution of cooperation.

In spite of agreement on this point, a seemingly interminable controversy persists because researchers often disagree bitterly about what constitutes a reasonable explanation for the required informational regularity. Genetic relatedness due to common ancestry provides an uncontroversial explanation (Hamilton, 1964). The details of genetic transmission ensure that two actors with the same parents, as one example, will on average be more similar to each other than two individuals randomly selected from the population. This is an example of an informational regularity that can support the evolution of cooperation, and cooperation among kin is well established, well understood, and widely accepted.

Reciprocal strategies can also generate the required regularity. Such strategies share the feature that a focal individual conditions her decision to cooperate in some way on information about current or potential partners. Conditional cooperation can arise from simple rules based on direct experience with a partner (Axelrod, 1984) or indirect experience (Nowak & Sigmund, 1998), and they can also involve subtle considerations that assign good or bad standing to a partner (Leimar, 1997; Panchanathan & Boyd, 2004; Nowak & Sigmund, 2005). Though reciprocal strategies can evolve under the right circumstances, they can also be vulnerable in many ways. They are often not especially robust as group size increases (Boyd & Richerson, 1988), when agents make errors

* Corresponding authors.

E-mail addresses: charles.efferson@econ.uzh.ch (C. Efferson), carlosp.roca@urv.cat (C.P. Roca), dhelbing@ethz.ch (D. Helbing).¹ Efferson and Roca contributed equally to this research.

(Nowak & Sigmund, 1993; Henrich, 2004; Nowak & Sigmund, 2005), or when the space of admissible strategies is sufficiently complex (Boyd & Lorberbaum, 1987; van Veelen, García, Rand, & Nowak, 2012).

In any case, with respect to human behavior the larger puzzle is that humans routinely cooperate with genetically unrelated individuals in situations where reciprocal behavior is either not possible or cannot produce future benefits for the reciprocator (Camerer, 2003; Fehr & Fischbacher, 2003; Henrich et al., 2006; Raihani & Bshary, 2015). This simple observation leads to questions of the following sort. Do humans cooperate with unrelated individuals because they are responding to a kinship-based psychology that is occasionally misapplied, or do humans have prosocial motives that evolved in part for reasons unrelated to genetic relatedness (Fehr & Henrich, 2003)? One can ask analogous questions about cooperation in anonymous one-shot interactions and the evolution of reciprocal strategies (Burnham & Johnson, 2005; Haley & Fessler, 2005; Hagen & Hammerstein, 2006; Burnham, 2013). Answers to these questions vary, but the upshot is that at least some researchers have concluded that conventional evolutionary explanations based on kinship and reciprocity are not sufficient to explain human cooperation in its entirety (Henrich, 2004; Boyd & Richerson, 2005; Bowles & Gintis, 2011).

Alternative explanations have been offered, and shared group affiliation in a structured population is a controversial one (Williams, 1966; Soltis, Boyd, & Richerson, 1995; Boyd & Richerson, 2005; Bowles, 2009; Boyd, Richerson, & Henrich, 2011). If variation in cooperation levels occurs mostly between groups, then individuals in the same group tend to be similar. Group affiliation in such a case is an important source of information. Interacting with a group affiliate increases the probability that a cooperator interacts with a cooperator, and it decreases the probability that a defector interacts a cooperator. The problem with shared group affiliation as a source of information, however, is maintaining variation between groups. In a strictly genetic system at least (cf. Boyd et al., 2011), selection within groups and migration will often eliminate most of the differences between groups (Henrich, 2004). This destroys the information associated with shared group affiliation, and in the end a randomly selected member of one's own group will be extremely similar, in expectation, to a randomly selected member of any group. Put differently, relatedness within groups should often be low (cf. Bell, Richerson, & McElreath, 2009; Hill et al., 2011).

The above reasoning holds when migration is global and unsystematic. If cooperators ever find themselves in groups of their own, migration of this sort will largely destroy this kind of grouping. What if, however, movement between groups is a biased process? Partner choice is an especially clear mechanism for generating biases in group formation (Noë & Hammerstein, 1995; Roberts, 1998; Raihani & Bshary, 2015). Unlike reciprocal strategies, which condition behavior on a current partner's recent behavior or reputation, partner choice conditions one's willingness to interact socially on a partner's recent behavior or reputation. To give an illustrative but somewhat unrealistic example, assume that cooperators, and only cooperators, always know of some new secret place to rendezvous if they face too much free-riding in their current groups. This means they can consistently sequester themselves, even if their secret places are eventually discovered, they can interact primarily with their fellow cooperators, and they can consistently enjoy the gains from mutual cooperation. Presumably this mechanism would support the evolution of cooperation, but it requires that cooperators have privileged access to crucial information. As with green beards (Dawkins, 1976) and image scores (Nowak & Sigmund, 1998; Wedekind & Milinski, 2000), the informational regularity that allows cooperators to limit exploitation is like a gift from heaven.

As this example suggests, however, effective partner choice can involve distinct mechanisms (Noë & Hammerstein, 1995). Specifically, one can opt out of a current relationship because one knows it is bad (Eguíluz, Zimmermann, Cela-Conde, & San Miguel, 2005; McNamara, Barta, Fromhage, & Houston, 2008; Roca & Helbing, 2011; Bednarik,

Fehl, & Semmann, 2014), one can opt in to a new relationship because of information suggesting the relationship might be good (Barclay & Willer, 2007), or one can do both (Rand, Arbesman, & Christakis, 2011; Wang, Suri, & Watts, 2012; Antonioni, Cacault, Lalive, & Tomassini, 2014). Opting in can lead to prosocial behavior because competition for partners can lead players to use current cooperation to signal that they would make good partners (Roberts, 1998; Barclay & Willer, 2007). For people looking to opt in to a new relationship, this mechanism requires that the current cooperation of a potential partner is a reliable and available source of information about the potential partner's future behavior. As always, this raises questions about where this reliable information comes from and how its integrity is maintained.

Opting out of an existing relationship is different. Opting out relies instead on one's recent personal experience. One does not need to know how a potential partner might behave. Rather one needs to know how current partners have been behaving. The informational requirements in this case are considerably less stringent than for opting in. Recent models suggest that opting out might work as a stand-alone mechanism (McNamara et al., 2008; Roca & Helbing, 2011), but we know little about how people actually use the option to leave others behind. In particular, we would like to know how effective is a situation in which players can opt out of their current relationships, but they have no information about the kinds of partners they will face after doing so. Put differently, how much cooperation results when players cannot run toward good behavior, but they can run away from bad behavior?

To find out, we conducted a behavioral experiment in which players were distributed on a lattice. In every period, each player had the option to move to a new location. After player movements, each player played a social dilemma game with all the players in her neighborhood. Crucially, information was very limited, and thus players faced considerable uncertainty when they moved. In particular, players were not identifiable as individuals, and their histories of play were not publicly available. Thus, a player who chose to move did not know with whom she would interact in her new location, nor whether her new partners were likely to cooperate. When a player moved, in short, she took a shot in the dark.

What a player did know was how she had fared in her past interactions. Specifically, a player knew how many partners she had recently played the game with, and she knew the payoffs she had received. Players could thus infer the total cooperation in their respective neighborhoods but little else. The key question is the following. When coupled with the option to migrate away from one's current neighborhood, can this kind of limited information allow players to avoid exploitation often enough to reduce or even eliminate the disadvantages of cooperating? If so, the result would show that non-random movement based on limited information could have been an important mechanism contributing to the evolution of human cooperation.

2. Experimental methods

Our experiment consisted of two treatments. To ease the exposition, we will first describe our main experimental treatment, the "choose location" treatment. Afterwards, we will describe the control, which we call the "assign location" treatment.

In the choose location treatment, each player was located somewhere on a 12×12 lattice. As explained below, sessions involved 31 or 35 participants, and as a result 20%–25% of available sites were occupied. Because of this low density, participants who wanted to move were not limited to recently vacated sites.

The lattice was on a torus, and thus no player was ever on an edge or corner. At the beginning of a period, each player saw the current state of the lattice (Fig. 1). She saw herself at the center of the lattice, and she saw which cells were occupied for the rest of the lattice. In addition, each player saw two neighborhoods of interest. She saw her eight-cell

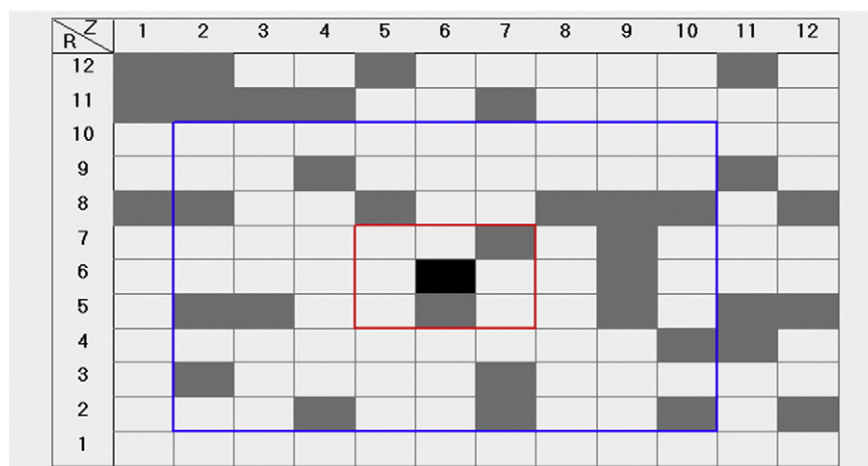


Fig. 1. Example lattice showing the state of the population. Players were placed on a torus, and so they experienced no edges or corners. To show the state of the population, the torus was displayed as a rectangle, where the focal decision maker was always shown in black in the middle of the lattice. Other players were shown in dark gray. The large blue rectangle represented the neighborhood within which the focal individual could migrate. The small red rectangle represented the neighborhood within which the focal individual played the social dilemma.

neighborhood, surrounded by a red line, and she saw her 80-cell neighborhood, surrounded by a blue line.

The 80-cell neighborhood was the player's "migration neighborhood." Specifically, the first decision a player made in a period was whether to try and move to a new location. If she did not want to move, the player would simply stay where she was. If she wanted to move, the player had to request a move to a currently unoccupied cell within her migration neighborhood. Because two or more players could have asked to move to the same cell, a requested move was not necessarily successful. If only a single player requested to move to a specific cell, the move was always implemented. If two or more players requested to move to the same cell, only one of them was randomly chosen to actually move. The others requesting the same cell stayed where they were for the period in question. That is, their requested moves were not successful. Because density was low, the majority of requests, though certainly not all, were successful (71.7% of 2844 requests).

After all movements took place, each player played a social dilemma game with everyone in her "social dilemma neighborhood." The social dilemma neighborhood was simply the neighborhood of eight cells around the focal player. Consequently, the eight-cell neighborhood shown at the beginning of each period (Fig. 1) depicted the focal player's social dilemma neighborhood if neither the focal player nor anyone else moved in or out.

If the focal player did not want to move in a period, she knew she would stay in her current location, and she made a binding choice for the social dilemma. If she wanted to move, as explained above, she first had to request a move to a currently unoccupied cell within her migration neighborhood. Because a requested move was not necessarily successful, a player requesting a move had to make two choices for the social dilemma. First, she had to make a choice for the case in which the requested move was successful. Second, she also had to make a choice for the case in which the requested move was unsuccessful. Hence, the choice actually implemented was dependent on whether or not the requested move was successful.

For the social dilemma itself, each player had an endowment, e . Possibly conditional on the success of a requested move, each player cooperated by contributing her entire endowment, or she defected by retaining it. If a player contributed her endowment, it was multiplied by $b = 2$, and the resulting amount was distributed equally among the focal player and all players in her social dilemma neighborhood after all movements were implemented. Regardless of whether or not a player retained her endowment, she received payments if others in her social dilemma neighborhood cooperated. If a player ended up alone with no one in her social dilemma neighborhood, she simply retained

her endowment regardless of her stated choice for the social dilemma. In this case, she could not play, and efficiency gains were not possible.

Specifically, let $n \in \{0, \dots, 8\}$ indicate the number of neighbors a focal player had after all movements were implemented. Given n neighbors, let $k \in \{0, \dots, n\}$ indicate the number of neighbors who cooperated. If a focal individual ended up by herself, then $n = 0$, and the individual simply retained her endowment and received e as a payoff. If $n \geq 1$, the payoff for cooperating was $\pi(C) = be(k + 1)/(n + 1)$, and the payoff for defecting was $\pi(D) = e + bek/(n + 1)$.

In sum, each player made two types of decision per period. First, a player chose whether to move. Second, she chose how to play the social dilemma. If the player did not want to move, she made a single decision to cooperate or defect. If she wanted to move, she made two decisions for the social dilemma game: one in case her requested move was successful, and the other in case her requested move was unsuccessful. Importantly, because each player played with everyone in her eight-cell neighborhoods, players were often members of multiple overlapping neighborhoods. If a player cooperated, her contribution was counted in all the social dilemma neighborhoods the player belonged to. To illustrate this, imagine that Abigail, Bernhard, Celia, and Douglas are lined up next to each other in adjacent cells from left to right. No one else is anywhere near them. In this configuration, Abigail and Douglas each have one neighbor, while Bernhard and Celia each have two. All of them cooperate. Because the contribution of any single player is applied separately in all her social dilemma neighborhoods, all four of them receive a payoff of be . In particular, the contributions of Bernhard and Celia are not diluted by the fact that they each belong to the social dilemma neighborhoods of two other players. This design feature ensured that having a partner with many partners is not an intrinsic disadvantage. If this had not been the case, all players would have faced incentives to be in small isolated neighborhoods. By extension, if reciprocity would have worked better with very few neighbors (Boyd & Richerson, 1988), such incentives could have inflated the rate of cooperation as a simple by-product of extreme population fragmentation. Our interest instead was in how movement can affect cooperation without incentives that directly favor small neighborhoods regardless of cooperation rates. For this reason a player's contribution was counted independently in all social dilemma neighborhoods the player belonged to.

After all decisions in a period were recorded, successful moves were implemented. Then, contingent decisions for the social dilemma were applied for all players, and payoffs were determined. In all periods but the first, in addition to the state of the lattice (Fig. 1), players received three explicit pieces of information at the beginning of each period. First, each player was told how many neighbors she had just played

the social dilemma with. Because the state of the lattice was carried over from the end of the last period to the beginning of the current period, this information was also available by simply inspecting the social dilemma neighborhood displayed on the lattice (Fig. 1). Second, each player was told how much she earned from playing the social dilemma game in the last period. Third, she was told her average payoff per period over all periods since her most recent move to her current location. As mentioned above, players were not individually identifiable, and their histories of play were not publicly available.

The procedures above were for the choose location treatment. The assign location treatment was identical apart from one small but critical difference. Specifically, each session of the assign location treatment was paired with a corresponding session of the choose location treatment. Choose location sessions were conducted first, and the number of subjects in an assign location session was identical to the number of subjects in the associated choose location session. All sessions ran for 100 periods. In each period of an assign location session, participants were randomly assigned to occupied locations, after movement, from the same period of the associated choose location session. This procedure was implemented independently in each period, and altogether our methods ensured that the topology of the social network and the spatial configurations of interaction neighborhoods were identical in all periods of paired sessions. The only difference was that network topology was endogenous in the choose location session and exogenous in the assign location session. We conducted two choose location sessions, one with 35 participants and the other with 31. Correspondingly, we conducted two assign location sessions with 35 and 31 participants.

All interactions were anonymous, and subjects were fully and accurately informed about the rules of the game. We conducted the experiment using z-Tree (Fischbacher, 2007) at the Decision Science Laboratory at the Swiss Federal Institute of Technology in Zurich (www.descil.ethz.ch). All choices were paid, with earnings accumulated over the 100 periods. Participants were paid privately in cash at the end of their respective sessions. The endowment in each period was 20 points, where one point was worth 1/60 of a Swiss Franc. For most of our analyses below, we will normalize the endowment to equal one. Participants received 10 Swiss Francs as a show-up fee, and the average total payment was 53.10 Swiss Francs.

3. Statistical methods

Our data consist of 13,200 observations. To analyze the data, we must account for two types of potential dependence among observations. First, we have 100 observations per player. Second, players interacted in partially overlapping neighborhoods that persisted through time in ways that depended on player movements. Previous research has shown that choices in social dilemmas are often conditional on the choices of others in the group (Fischbacher, Gaechter, & Fehr, 2001), and in our experiment this kind of conditional play could have generated choices that were correlated across subjects. In terms of data analysis, the key to this kind of dependence is that the groups in our experiment were partially overlapping, and they were not fixed. As a result, dependencies could have existed between players who were either directly or indirectly linked, and these dependencies tended to change over time because players moved. The freedom to move is precisely what provided participants with the possibility to leave neighborhoods they did not like. In terms of data analysis, however, it means we must begin by identifying the loci of potentially correlated choices in the social dilemma game.

To do so, we used our data to identify “persistent network clusters” (see electronic supplementary materials, available on the journal's website at www.ehbonline.org). Each persistent network cluster was a subset of player–period combinations. Such a subset was characterized by the potential for dependencies in choice to propagate across players through time as players moved on the lattice and played the social dilemma. Each persistent network cluster persisted for one or more periods. To identify persistent network clusters, we partitioned the set of

players in each period according to the connected components in the social network. We then linked the resulting subsets across periods according to the similarities between subsets. This captures the idea that network clusters persisted through time. Importantly, we implemented a very conservative approach in the sense that any potential for dependence, both across individuals and through time, was accounted for by coding all relevant observations as part of the same persistent network cluster (electronic supplementary materials, available on the journal's website at www.ehbonline.org).

To account fully for both sources of dependence in our disaggregated data, associated regression results and statistical tests used standard errors calculated by clustering jointly on both experimental subject and persistent network cluster. Clustered standard errors allow for an arbitrary degree of dependence within a cluster, but the calculations assume that observations across clusters are independent (Verbeek, 2008). Two-way clustering is simply a generalization of this approach that allows for two different sources of dependence (Arai, 2011; Cameron, Gelbach, & Miller, 2011). In our case, these two sources of dependence were repeated observations per participant and the correlations in choices that can occur when participants play social dilemma games in partially overlapping neighborhoods.

4. Results

When modeling the social dilemma choices actually implemented over all observations, we found that players in the choose location treatment cooperated significantly more than players in the assign location treatment (Fig. 2, logistic regression with two-way clustering, $p < 0.001$). Moreover, when participants in the choose location treatment requested a move, they stated that they wanted to cooperate significantly more if the move was successful than if the move was unsuccessful. More precisely, conditioning on the 2844 cases in which subjects requested to move in the choose location treatment, players stated a desire to cooperate 37.76% of the time if a requested move was successful but only 24.61% of the time if unsuccessful (logistic regression with two-way clustering, $p < 0.001$).

Conditioning one's current behavior on the success of a requested move was a pattern almost entirely due to players who had recently cooperated. Specifically, if we exclude the first period of choose location sessions, we are left with 2696 observations involving a subject who cooperated in the previous period and 3838 observations involving a subject who defected in the previous period. In both cases, players requested to move when their payoffs were low. For players who cooperated in the previous period, they were more likely to request a

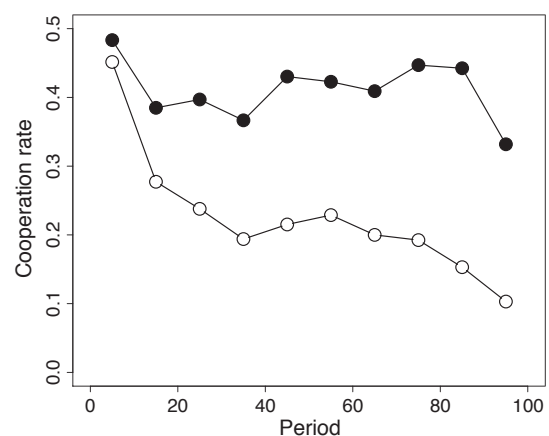


Fig. 2. Cooperation rates by treatment. Solid circles represent the choose location treatment, while open circles show data from the assign location treatment. Using a logistic regression with standard errors clustered on both experimental subjects and persistent network clusters, the estimated coefficient for the choose location dummy is 0.877 ($p < 0.001$). Choices were aggregated over blocks of ten periods to produce the graph.

move in the current period if their payoff in the previous period was relatively low (logistic regression with two-way clustering, estimated coefficient for lagged non-normalized profit: $-0.066, p < 0.001$). The same pattern was true for players who defected in the previous period (logistic regression with two-way clustering, estimated coefficient for lagged non-normalized profit: $-0.048, p < 0.001$).

Unlike players who defected in the previous period, however, players who cooperated were sensitive to the success of the requested move. For the 1026 cases in which subjects requested a move and cooperated in the previous period, players wanted to cooperate 77.68% of the time if the requested move was successful but only 47.95% of the time if unsuccessful (logistic regression with two-way clustering, $p < 0.001$). In contrast, for the 1786 cases in which subjects requested a move and defected in the previous period, players wanted to cooperate 14.56% of the time if the requested move was successful and 10.97% of the time if unsuccessful (logistic regression with two-way clustering, $p = 0.263$). These results show that, once a recently cooperative player decided it was time to move, she was more willing to continue cooperating if she was actually able to move compared to the situation when she was not able to move. The same distinction between successful and unsuccessful moves did not hold for players who did not cooperate in the most recent period.

Most importantly, players used endogenous movement in the choose location treatment to eliminate a payoff disadvantage that was initially associated with cooperating. This payoff disadvantage occurred and persisted in our assign location treatment, but in the choose location treatment it declined through time until it disappeared altogether (Table 1 and Fig. 3A–B). Indeed, over the last 50 periods of the choose location treatment, cooperating produced the same payoffs on average as defecting ($p = 0.941$, see Fig. 3B), where averages are over all subjects within a period regardless of neighborhood composition. This kind of convergence in average payoffs did not occur in the assign location treatment (Table 1). Moreover, these results cannot be due to differences between the two treatments in terms of social network topology. The design of the assign location treatment guaranteed that such differences would not exist. Altogether, our results indicate that participants in the choose location treatment used endogenous movement to eliminate on average the payoff disadvantage of cooperating compared to defecting. Participants subject to exogenous movement in the assign location treatment did not or could not do this.

To understand why this treatment difference occurred, we need to understand the forces that controlled payoffs associated with cooperating and defecting. Decomposing the difference between the average payoff of cooperation and the average payoff of defection allows us to identify these forces. For this decomposition, let $x_{it} \in \{C, D\}$ denote the choice implemented for individual $i \in \{1, \dots, J\}$ in time period $t \in$

$\{1, \dots, 100\}$. We define c_{it} as the indicator function of player i cooperating in period t ,

$$c_{it} = \begin{cases} 1 & \text{if } x_{it} = C, \\ 0 & \text{if } x_{it} = D. \end{cases}$$

The corresponding indicator function for defecting is $1 - c_{it}$.

Let N_{it} be the number of individuals who were in the social dilemma neighborhood of a focal player. Analogously, let K_{it} be the number of cooperators who were among these N_{it} neighbors. We use the Kronecker delta to identify observations for which the number of neighbors, N_{it} , and the number of cooperative neighbors, K_{it} , equaled specific values,

$$\delta_{N_{it}n} = \begin{cases} 1 & \text{if } N_{it} = n, \\ 0 & \text{if } N_{it} \neq n, \end{cases} \quad \delta_{K_{it}k} = \begin{cases} 1 & \text{if } K_{it} = k, \\ 0 & \text{if } K_{it} \neq k. \end{cases}$$

With these quantities defined, the mean payoff in t for cooperating in a given treatment was

$$\bar{\pi}_t(C) = \frac{\sum_{i=1}^I c_{it} \left\{ e \delta_{N_{it}0} + \sum_{n=1}^8 \sum_{k=0}^n \frac{be(k+1)}{n+1} \delta_{N_{it}n} \delta_{K_{it}k} \right\}}{\sum_{i=1}^I c_{it}}$$

Analogously, the mean payoff in t for defecting in a given treatment was

$$\bar{\pi}_t(D) = \frac{\sum_{i=1}^I (1 - c_{it}) \left\{ e + \sum_{n=1}^8 \sum_{k=0}^n \frac{bek}{n+1} \delta_{N_{it}n} \delta_{K_{it}k} \right\}}{\sum_{i=1}^I (1 - c_{it})}$$

The difference in the mean payoff of cooperation and the mean payoff of defection can be decomposed as $\bar{\pi}_t(C) - \bar{\pi}_t(D) = e(s_t + a_t + g_t)$.

The quantity s_t is a “small group” effect of the form,

$$s_t = \frac{\sum_{i=1}^I \sum_{n=1}^8 \sum_{k=0}^n \frac{b}{n+1} c_{it} \delta_{N_{it}n} \delta_{K_{it}k}}{\sum_{i=1}^I c_{it}}$$

Conditional on being in a group with at least one other person, s_t captures how strongly participants who cooperated in t gained an advantage over those who defected by moving into small groups and thus obtaining a relatively large fraction, $b/(n+1)$, of the benefits generated by their own contributions. If at least one player cooperated in t in any session for a given treatment, which was always true, then s_t is well defined, and it must be positive.

The quantity a_t is an “assortment” effect, where

$$a_t = \frac{\sum_{i=1}^I \sum_{n=1}^8 \sum_{k=0}^n \frac{bk}{n+1} c_{it} \delta_{N_{it}n} \delta_{K_{it}k}}{\sum_{i=1}^I c_{it}} - \frac{\sum_{i=1}^I \sum_{n=1}^8 \sum_{k=0}^n \frac{bk}{n+1} (1 - c_{it}) \delta_{N_{it}n} \delta_{K_{it}k}}{\sum_{i=1}^I (1 - c_{it})}$$

Conditional on being in a group with at least one other person, the assortment effect measures the extent to which participants who cooperated in t , compared to those who defected, assorted themselves into neighborhoods with other participants who were also cooperating. If at least one player cooperated and at least one defected in t in any session for a treatment, which was always true, then a_t is well defined. It can take negative values, positive values, or a value of zero. Specifically, because $bk/(n+1)$ appears in both terms, $a_t > 0$ means that cooperating

Table 1
Payoffs by treatment and behavior.

Parameter	$t \geq 1$			$t \geq 51$		
	Estimate	Std. error	p	Estimate	Std. error	p
Intercept	1.282	0.019	<0.001	1.210	0.011	<0.001
Coop	-0.326	0.040	<0.001	-0.280	0.027	<0.001
Choose	0.130	0.033	<0.001	0.160	0.037	<0.001
Coop \times Choose	0.240	0.077	0.002	0.284	0.052	<0.001

Results are from OLS regressions with profit as the response variable. Profit is normalized in the sense that we calibrated the endowment to equal 1. Independent variables include a dummy indicating if the subject cooperated for a given choice, a dummy indicating if the subject was in the choose location treatment, and the interaction of these two dummies. We fit the model separately to the entire data set (13,200 observations) and to the data from periods 51 to 100 (6600 observations). Standard errors were calculated by clustering on both subject and persistent network cluster. The significantly negative effects for “Coop” show that cooperation reduced payoffs in the assign location treatment. Fig. 3 presents additional analyses, in particular a test showing how cooperation and defection produced the same average payoffs in the latter half of choose location sessions.

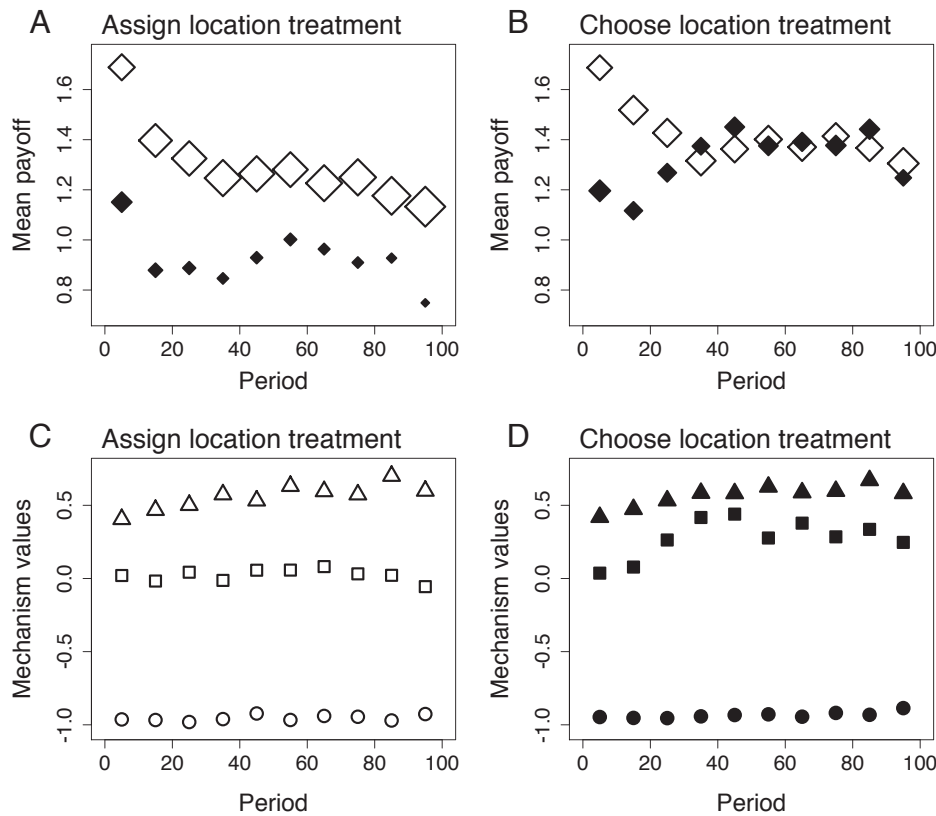


Fig. 3. Average payoffs for cooperating and defecting. The upper panels show the average payoffs for defecting (open diamond) and cooperation (solid diamond), and the relative sizes of the symbols represent the relative proportions of the two behaviors across period–subject combinations. Panel A shows that, in the assign location treatment, cooperating resulted in a significant payoff disadvantage (Table 1). In contrast, panel B shows that endogenous movement equalized the average payoffs associated with cooperating and defecting in the choose location treatment. The simplest approach to testing this is to model payoffs with a regression that restricts attention to periods $t \geq 51$ of the choose location treatment. Doing so, with two-way clustering, produces an estimated effect for cooperation of 0.003 ($p = 0.941$). The lower panels decompose the difference in payoffs between cooperation and defection into the small group effect (triangles), the assortment effect (squares), and retain endowment effect (circles). Panel C shows the assign location treatment, while panel D shows the choose location treatment. Comparing the decomposition across treatments (C vs. D) shows that cooperating players eliminated the disadvantage of cooperating in the choose location treatment (B) but not the assign location treatment (A) specifically because assortment differed by treatment (Table 2). For producing the graphs, observations were aggregated over blocks of ten periods.

players were in neighborhoods with other cooperators more on average than defecting participants were in neighborhoods with cooperators. In contrast, $a_t < 0$ would show that cooperating participants were in neighborhoods with other cooperators less on average than defecting participants were. Finally, $a_t = 0$ would indicate that players were not assorted by choice in t .

Finally, g_t is the “retain endowment” effect, where

$$g_t = \frac{\sum_{i=1}^I c_{it} \delta_{N_{it}0}}{\sum_{i=1}^I c_{it}} - 1.$$

The retain endowment effect captures the different rates at which participants who chose cooperation in t kept their endowments compared to those who chose defection. Participants who chose cooperation only retained their endowments if they ended up alone after all movements and thus could not play the game. Players who chose defection always retained their endowments, a fact captured by the -1 in the definition of g_t . Because defecting always meant that a player retained her endowment, while this was not true when cooperating, g_t must be non-positive.

To see how players eliminated the payoff disadvantage of cooperating compared to defecting in the choose location treatment, we calculated the small group, assortment, and retain endowment effects for each period of each treatment. Importantly, $e(s_t + a_t + g_t)$ is an exact decomposition of the difference in average payoffs for

cooperating versus defecting. The decomposition requires no assumptions; it simply expresses this difference in a particularly useful way. For the calculations, we conditioned only on period and treatment. We did not condition, in particular, on group composition. Indeed, doing so would run counter to the purpose of the analysis because s_t , a_t , and g_t all summarize, in different ways, payoff effects that were due to group composition.

In sum, our empirical strategy was to compare, across the two treatments, the dynamics of each constituent force. Because $e(s_t + a_t + g_t)$ is an exact decomposition, and because a treatment effect did in fact occur (Table 1 and Fig. 3A–B), at least one of the forces must have differed, though perhaps not significantly, across treatments. Correspondingly, by comparing s_t , a_t , and g_t across treatments, we hoped to identify exactly how subjects drove $\bar{\pi}_t(C) - \bar{\pi}_t(D)$ from negative values up to zero in the choose location treatment but not in the assign location treatment.

The analysis showed that assortment was the key difference between our two treatments. Players in the choose location treatment were able to eliminate on average the payoff disadvantage of cooperation, while players in the assign location treatment were not, because movement in the choose location treatment generated positive assortment (Fig. 3D). This kind of assortment was absent in the assign location treatment (Fig. 3C). All in all, the dynamics of the retain endowment effect and the small group effect were statistically indistinguishable in the two treatments, while the assortment dynamics were highly significantly different across the two treatments (Table 2).

Crucially, even though information was limited, positive assortment developed through time in the choose location treatment because cooperating players did not move in the same way as defecting players.

Table 2
Decomposition of differences in average payoffs between cooperating and defecting.

Parameter	Estimate	Std. error	<i>p</i>
Small group (<i>s_t</i>)			
Intercept	0.381	0.022	<0.001
<i>t</i>	0.006	0.001	<0.001
<i>t</i> ²	-3.475×10^{-5}	1.438×10^{-5}	0.017
Choose	0.011	0.035	0.749
<i>t</i> × Choose	5.286×10^{-4}	0.002	0.779
<i>t</i> ² × Choose	-8.866×10^{-6}	1.909×10^{-5}	0.643
Assortment (<i>a_t</i>)			
Intercept	-0.083	0.024	<0.001
<i>t</i>	0.005	0.001	<0.001
<i>t</i> ²	-4.637×10^{-5}	1.101×10^{-5}	<0.001
Choose	0.013	0.054	0.813
<i>t</i> × Choose	0.011	0.003	<0.001
<i>t</i> ² × Choose	-8.703×10^{-5}	2.597×10^{-5}	0.001
Retain endowment (<i>g_t</i>)			
Intercept	-0.973	0.011	<0.001
<i>t</i>	4.471×10^{-4}	7.467×10^{-4}	0.550
<i>t</i> ²	-1.288×10^{-6}	8.394×10^{-6}	0.878
Choose	0.026	0.014	0.063
<i>t</i> × Choose	-6.928×10^{-4}	9.633×10^{-4}	0.473
<i>t</i> ² × Choose	9.057×10^{-6}	1.078×10^{-5}	0.402

Results are from OLS regressions that model the dynamics of the small group (*s_t*), assortment (*a_t*), and retain endowment effects (*g_t*). Standard errors are calculated according to Newey & West (1987), a method assuming an error structure that is heteroskedastic and has possible autocorrelations up to some specified lag. We specified a maximal lag of 10. Independent variables include first-order and second-order period terms, both with and without a treatment dummy. Because assortment is the only mechanism with dynamics that differ significantly by treatment (*a_t*: *t* × Choose and *t*² × Choose), the difference in $\bar{\pi}_t(C) - \bar{\pi}_t(D)$ between treatments (Fig. 3A–B) can be traced to a difference in assortment dynamics between the treatments (Fig. 3C–D).

For all *t* > 1 in the choose location treatment, players cooperating in *t* did so after moving to a new location at a rate that was negatively related to the proportion of players who cooperated in their *t*-1 social dilemma neighborhoods (electronic supplementary materials, Table S1, available on the journal's website at www.ehbonline.org, logistic regression with two-way clustering, *p* < 0.001).² This means that, for players cooperating in *t*, they often did so in new neighborhoods after leaving a neighborhood with a relatively low proportion of cooperators. In contrast, they often stayed put and cooperated in the same locations if their neighborhoods had a relatively high proportion of cooperators. For players defecting in *t*, their realized movements were not systematically related to the rates of cooperation in their neighborhoods from the previous period (electronic supplementary materials, Table S1, available on the journal's website at www.ehbonline.org, logistic regression with two-way clustering, *p* = 0.318).

Cooperators and defectors also moved differently in terms of how they responded to neighborhood size. Players defecting in *t* showed a significant tendency to move away from relatively small *t*-1 neighborhoods (electronic supplementary materials, Table S2, available on the journal's website at www.ehbonline.org, logistic regression with two-way clustering, *p* < 0.001). Because of a weak but highly significant negative relation between the size of neighborhoods and the proportion of cooperators (electronic supplementary materials, Table S3, available on the journal's website at www.ehbonline.org, OLS regression with two-way clustering, *p* < 0.001), movement away from relatively small neighborhoods suggests that defecting players may have inadvertently moved away from cooperative neighborhoods. Players cooperating in *t*, in contrast, did not show a significant relationship between movement and the size of their social dilemma neighborhoods in the previous period (electronic supplementary materials, Table S2, available on the journal's website at www.ehbonline.org, logistic regression with two-way clustering, *p* = 0.078). Importantly, however, these differences in

² Players were not told about the proportion of cooperators in their past neighborhoods, but they could draw aggregate inferences from their payoffs.

movement cannot be attributed to differences in the rate of movement. For *t* > 1, the overall rates of actual movement in the choose location treatment were not related to player choices. Cooperating players moved 32.03% of the time, while defecting players moved 30.07% of the time (logistic regression with two-way clustering, *p* = 0.540). Moreover, both cooperating and defecting players significantly increased their rates of movement through time (electronic supplementary materials, Table S4, available on the journal's website at www.ehbonline.org, logistic regressions with two-way clustering, *p* < 0.001). This means that cooperating players did not move more than defecting players; they simply moved in a different way. In particular, assortment developed endogenously in the choose location treatment because cooperating individuals ran away from bad behavior, while defecting individuals did not.

5. Discussion

Our results show that the option to emigrate from one's current neighborhood can dramatically attenuate the individual-level forces that would otherwise oppose cooperation. Specifically, players in our choose location treatment used movement to assort themselves, statistically speaking, into relatively cooperative neighborhoods. Moreover, as assortment developed, it meant that cooperators were increasingly shielded from free-riding, and the average payoffs from cooperating correspondingly increased. Through time participants managed to entirely eliminate the initial disadvantage associated with cooperating. Finally, all of this happened even though players did not have information about the kinds of social interaction they would have if they moved. These results show more broadly that moving away from uncooperative behavior has the potential to significantly reduce or eliminate the force of individual selection against cooperation.

Importantly, moving in our experiment did not involve an explicit cost. If a participant happened to move from one neighborhood to a worse neighborhood, she may have paid an opportunity cost depending on the movements of others. Participants did not, however, have to hand over points to move. We thus do not know how an explicit cost would have affected our results. Cooperating players did not move more than defecting players in our choose location treatment; they just moved in a way that was especially sensitive to neighborhood composition. This at least suggests the possibility that adding an explicit cost could reduce the average payoff of cooperating and defecting by similar amounts. Moreover, a recent study by Bednarik et al. (2014) showed that increasing the cost of switching to a new partner lowered the rate of partner switching, but it did not decrease cooperation. Apparently, the mere threat of cutting social ties was enough to keep would-be defectors in line. This result further suggests that the effects of running away from bad behavior could be robust in the face of explicit costs. This is speculation, however, and the limits of partner choice with different kinds of explicit costs would benefit from additional empirical research.

We also do not know how effective the mechanism would be as the scale of social interactions increases. As with most behavioral experiments, including experiments on partner choice (Barclay & Willer, 2007; Rand et al., 2011; Wang et al., 2012; Antonioni et al., 2014; Bednarik et al., 2014), social groups in our experiment were relatively small. Human cooperation is distinctive in that it occurs at large scales with low genetic relatedness, and the evolution of this kind of large-scale cooperation may require special mechanisms (Boyd et al., 2011; Richerson et al., 2015).

In any case, we would like to emphasize that the option to migrate away from one's neighborhood in the choose location treatment did not make cooperation superior in terms of expected payoffs. Instead, it eliminated the difference in average payoffs between cooperating and defecting, and this in turn allowed players with an interest in cooperating to do so without paying any cost on average. The result was a stable mix of cooperation and defection over an extended period of time. Roughly between periods 10 and 90, the rate of cooperation in

the choose location treatment was stable at around 40%. This result demonstrates that, if people with some preference for cooperating are present, running away from bad behavior can allow them to express this preference without an associated disadvantage. With respect to the broader evolutionary question, our results also suggest how endogenous movement might interact with other forces. In particular, because endogenous movement neutralized the selective disadvantage of cooperation in the choose location treatment, it created the kind of situation that could allow other forces to play a decisive role.

One candidate force is group competition. With the individual-level costs of cooperation out of the picture, selection at higher levels of hierarchical organization can have relatively larger effects. Cultural transmission, in particular, has received considerable attention as a mechanism that can intensify the importance of selection at the group level (Henrich, 2004; Richerson & Boyd, 2005; Bell et al., 2009; Bowles & Gintis, 2011; Boyd et al., 2011; Richerson et al., 2015). Another candidate force is increased information, which could make movement more effective. In our experiment, participants were given no individual-specific information about the choices and payoffs of other players. As a result, movement was a blunt mechanism. In this setting, a player could not use movement to discipline only individuals who were defecting. Leaving an entire group behind in order to end a relationship with someone who was defecting also meant abandoning those in the group who were cooperating. This is analogous to the notion that reciprocity is hard to sustain in large groups because withdrawing cooperation punishes everyone in the group, defectors and cooperators alike (Boyd & Richerson, 1988).

In contrast, reliable information about the choices of specific players might have allowed cooperative individuals to use movement in a targeted fashion (Helbing & Yu, 2009). More generally, significant amounts of reliable information should be especially helpful if players are not simply restricted to controlling whom they interact with by moving around in space, but they can instead use the information more broadly to create and sever social ties. Other experiments show that this kind of mechanism can support cooperation (Rand et al., 2011; Wang et al., 2012). The mechanism, however, does rely on considerable amounts of reliable information about the reputations of others. As discussed in the introduction, reliable information supports the evolution of cooperation, but it also leads to fundamental questions about where the information comes from and why its reliability persists (Antonioni et al., 2014).

For this reason, we restricted our study to information derived from direct experience. A subject could infer aggregated information about her recent partners, but she had no information about whom she would meet or what was likely to happen if she moved. In this sense, our study excluded third-party information whose reliability was exogenously assured (Nowak & Sigmund, 1998; Fehr & Gaechter, 2002; Panchanathan & Boyd, 2004; Rand et al., 2011). We did not do this because we think information of this sort is never relevant. Rather, we wanted to see how far limited information based on direct experience can go in terms of supporting cooperation. Information based on direct experience is unproblematic precisely because it is readily available to the individual. Our results show that this kind of limited information, when coupled with endogenous movement, can play a pivotal role in supporting cooperation via its ability to attenuate or even eliminate the individual costs of cooperation.

Acknowledgments

D. H. would like to thank the European Research Council for its valued support in the form of an Advanced Investigator Grant, "Momentum" (Grant No.~324247). C. E. and S. V. would like to thank the Swiss National Science Foundation (Grant No. 100014-130127/1). The funders played no role in study design, data collection and analysis, the decision to publish, or preparation of the manuscript.

References

- Antonioni, A., Cacalet, M. P., Lalive, R., & Tomassini, M. (2014). Know thy neighbor: Costly information can hurt cooperation in dynamic networks. *PLoS ONE*, 9(10), e110788. <http://dx.doi.org/10.1371/journal.pone.0110788>.
- Arai, M. (2011). *Cluster-robust standard errors using R*. (<http://people.su.se/ma/clustering.pdf>).
- Axelrod, R. M. (1984). *The evolution of cooperation*. New York: Basic Books.
- Barclay, P., & Willer, R. (2007). Partner choice creates competitive altruism in humans. *Proceedings of the Royal Society of London B: Biological Sciences*, 274(1610), 749–753.
- Bednarik, P., Fehr, K., & Semmann, D. (2014). Costs for switching partners reduce network dynamics but not cooperative behaviour. *Proceedings of the Royal Society of London B*, 281(1792), 20141661.
- Bell, A. V., Richerson, P. J., & McElreath, R. (2009). Culture rather than genes provides greater scope for the evolution of large-scale human prosociality. *Proceedings of the National Academy of Sciences*, 106(42), 17671–17674.
- Bowles, S. (2009). Did warfare among ancestral hunter-gatherers affect the evolution of human social behaviors? *Science*, 324(5932), 1293–1298.
- Bowles, S., & Gintis, H. (2011). *A cooperative species: Human reciprocity and its evolution*. Princeton: Princeton University Press.
- Boyd, R., & Lorberbaum, J. P. (1987). No pure strategy is evolutionarily stable in the repeated prisoner's dilemma game. *Nature*, 327, 58–59.
- Boyd, R., & Richerson, P. J. (1988). The evolution of reciprocity in sizable groups. *Journal of Theoretical Biology*, 132(3), 337–356.
- Boyd, R., & Richerson, P. J. (2005). *The origin and evolution of cultures*. Oxford: Oxford University Press.
- Boyd, R., Richerson, P. J., & Henrich, J. (2011). Rapid cultural adaptation can facilitate the evolution of large-scale cooperation. *Behavioral Ecology and Sociobiology*, 65(3), 431–444.
- Burnham, T. C. (2013). Toward a neo-Darwinian synthesis of neoclassical and behavioral economics. *Journal of Economic Behavior & Organization*, 90(Supplement), S113–S127 (Evolution as a General Theoretical Framework for Economics and Public Policy).
- Burnham, T. C., & Johnson, D. D. P. (2005). The biological and evolutionary logic of human cooperation. *Analyse & Kritik*, 27(2), 113–135.
- Camerer, C. F. (2003). *Behavioral game theory: Experiments in strategic interaction*. Princeton: Princeton University Press.
- Cameron, A. C., Gelbach, J. B., & Miller, D. L. (2011). Robust inference with multiway clustering. *Journal of Business & Economic Statistics*, 29(2), 238–249.
- Dawkins, R. (1976). *The selfish gene*. Oxford: Oxford University Press.
- Eguíluz, V. M., Zimmermann, M. G., Cella-Conde, C. J., & San Miguel, M. (2005). Cooperation and the emergence of role differentiation in the dynamics of social networks. *American Journal of Sociology*, 110(4), 977–1008.
- Fehr, E., & Fischbacher, U. (2003). The nature of human altruism. *Nature*, 425, 785–791.
- Fehr, E., & Gaechter, S. (2002). Altruistic punishment in humans. *Nature*, 415, 137–140.
- Fehr, E., & Henrich, J. (2003). Is strong reciprocity a maladaptation? On the evolutionary foundations of human altruism. In P. Hammerstein (Ed.), *Genetic and Cultural Evolution of Cooperation* (pp. 55–82). Cambridge: The MIT Press.
- Fischbacher, U. (2007). z-Tree: Zurich toolbox for ready-made economic experiments. *Experimental Economics*, 10(2), 171–178.
- Fischbacher, U., Gaechter, S., & Fehr, E. (2001). Are people conditionally cooperative? Evidence from a public goods experiment. *Economic Letters*, 71(3), 397–404.
- Frank, S. A. (1998). *Foundations of social evolution*. Princeton: Princeton University Press.
- Hagen, E. H., & Hammerstein, P. (2006). Game theory and human evolution: A critique of some recent interpretations of experimental games. *Theoretical Population Biology*, 69(3), 339–348.
- Haley, K. J., & Fessler, D. M. T. (2005). Nobody's watching?: Subtle cues affect generosity in an anonymous economic game. *Evolution and Human Behavior*, 26(3), 245–256.
- Hamilton, W. D. (1964). The genetical evolution of social behavior. *Journal of Theoretical Biology*, 7(1), 1–52.
- Helbing, D., & Yu, W. (2009). The outbreak of cooperation among success-driven individuals under noisy conditions. *Proceedings of the National Academy of Sciences*, 106(10), 3680–3685.
- Henrich, J. (2004). Cultural group selection, coevolutionary processes and large-scale cooperation. *Journal of Economic Behavior and Organization*, 53(1), 3–35.
- Henrich, J., McElreath, R., Barr, A., Ensminger, J., Barrett, C., Bolyanatz, A., et al. (2006). Costly punishment across human societies. *Science*, 312(5781), 1767–1770.
- Hill, K. R., Walker, R. S., Božičević, M., Eder, J., Headland, T., Hewlett, B., et al. (2011). Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science*, 331(6022), 1286–1289.
- Leimar, O. (1997). Repeated games: A state space approach. *Journal of Theoretical Biology*, 184(4), 471–498.
- McNamara, J. M., Barta, Z., Fromhage, L., & Houston, A. I. (2008). The coevolution of choosiness and cooperation. *Nature*, 451, 189–192.
- Newey, W. K., & West, K. D. (1987). A simple, positive semi-definite, heteroskedasticity and autocorrelation consistent covariance matrix. *Econometrica*, 55(3), 703–708.
- Noë, R., & Hammerstein, P. (1995). Biological markets. *Trends in Ecology & Evolution*, 10(8), 336–339.
- Nowak, M. A. (2006). Five rules for the evolution of cooperation. *Science*, 314(5805), 1560–1563.
- Nowak, M. A., & 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.
- Nowak, M. A., & Sigmund, K. (1998). The dynamics of indirect reciprocity. *Journal of Theoretical Biology*, 194(4), 561–574.
- Nowak, M. A., & Sigmund, K. (2005). Evolution of indirect reciprocity. *Nature*, 437, 1291–1298.

- Panchanathan, K., & Boyd, R. (2004). Indirect reciprocity can stabilize cooperation without the second-order free rider problem. *Nature*, *432*, 499–502.
- Raihani, N. J., & Bshary, R. (2015). Why humans might help strangers. *Frontiers in Behavioral Neuroscience*, *9*(39).
- Rand, D. G., Arbesman, S., & Christakis, N. A. (2011). Dynamic social networks promote cooperation in experiments with humans. *Proceedings of the National Academy of Sciences*, *108*(48), 19193–19198.
- Richerson, P. J., Baldini, R., Bell, A., Demps, K., Frost, K., Hillis, V., et al. (2015). Cultural group selection plays an essential role in explaining human cooperation: A sketch of the evidence. *Behavioral and Brain Sciences*, <http://dx.doi.org/10.1017/S0140525X1400106X> (in press).
- Richerson, P. J., & Boyd, R. (2005). *Not by genes alone: How culture transformed the evolutionary process*. Chicago: University of Chicago Press.
- Roberts, G. (1998). Competitive altruism: From reciprocity to the handicap principle. *Proceedings of the Royal Society of London B: Biological Sciences*, *265*(1394), 427–431.
- Roca, C. P., & Helbing, D. (2011). Emergence of social cohesion in a model society of greedy, mobile individuals. *Proceedings of the National Academy of Sciences*, *108*(28), 11370–11374.
- Soltis, J., Boyd, R., & Richerson, P. J. (1995). Can group-functional behaviors evolve by cultural group selection?: An empirical test. *Current Anthropology*, *36*(3), 473–494.
- van Veelen, M. (2009). Group selection, kin selection, altruism and cooperation: When inclusive fitness is right and when it can be wrong. *Journal of Theoretical Biology*, *259*(3), 589–600.
- van Veelen, M., García, J., Rand, D. G., & Nowak, M. A. (2012). Direct reciprocity in structured populations. *Proceedings of the National Academy of Sciences*, *109*(25), 9929–9934.
- Verbeek, M. (2008). *A guide to modern econometrics* (3rd ed.). West Sussex, England: John Wiley & Sons, Ltd.
- Wang, J., Suri, S., & Watts, D. J. (2012). Cooperation and assortativity with dynamic partner updating. *Proceedings of the National Academy of Sciences*, *109*(36), 14363–14368.
- Wedekind, C., & Milinski, M. (2000). Cooperation through image scoring in humans. *Science*, *288*(5467), 850–852.
- Williams, G. C. (1966). *Adaptation and natural selection*. Princeton: Princeton University Press.