Contents lists available at ScienceDirect







journal homepage: www.elsevier.com/locate/jtbi

# Indirect reciprocity with negative assortment and limited information can promote cooperation



## Eleanor Brush<sup>a,b,\*</sup>, Åke Brännström<sup>a,c</sup>, Ulf Dieckmann<sup>a</sup>

<sup>a</sup> Evolution and Ecology Program, International Institute for Applied Systems Analysis, Laxenburg, A-2361, Austria <sup>b</sup> Program in Quantitative and Computational Biology, Princeton University, Princeton, NJ 08544, USA

<sup>c</sup>Department of Mathematics and Mathematical Statistics, Umeå University, Umeå, 901 87, Sweden

#### ARTICLE INFO

Article history: Received 26 April 2017 Revised 15 November 2017 Accepted 8 January 2018 Available online 11 January 2018

Keywords: Evolution Game theory Knowledge Replicator dynamics Reputation

#### ABSTRACT

Cooperation is ubiquitous in biological and social systems, even though cooperative behavior is often costly and at risk of exploitation by non-cooperators. Several studies have demonstrated that indirect reciprocity, whereby some members of a group observe the behaviors of their peers and use this information to discriminate against previously uncooperative agents in the future, can promote prosocial behavior. Some studies have shown that differential propensities of interacting among and between different types of agents (interaction assortment) can increase the effectiveness of indirect reciprocity. No previous studies have, however, considered differential propensities of observing the behaviors of different types of agents (information assortment). Furthermore, most previous studies have assumed that discriminators possess perfect information about others and incur no costs for gathering and storing this information. Here, we (1) consider both interaction assortment and information assortment, (2) assume discriminators have limited information about others, and (3) introduce a cost for information gathering and storage, in order to understand how the ability of discriminators to stabilize cooperation is affected by these steps toward increased realism. We report the following findings. First, cooperation can persist when agents preferentially interact with agents of other types or when discriminators preferentially observe other discriminators, even when they have limited information. Second, contrary to intuition, increasing the amount of information available to discriminators can exacerbate defection. Third, introducing costs of gathering and storing information makes it more difficult for discriminators to stabilize cooperation. Our study is one of only a few studies to date that show how negative interaction assortment can promote cooperation and broadens the set of circumstances in which it is know that cooperation can be maintained.

© 2018 Elsevier Ltd. All rights reserved.

#### 1. Introduction

The persistence of cooperation in biological and social systems is an evolutionary puzzle, because one would naively expect that, among cooperators who contribute their own resources to help other members of their group and defectors who do not, the defectors will do better and increase in numbers at the expense of the cooperators. This intuition is captured by simple models of evolutionary game theory predicting the demise of cooperation and the domination of defection. Nevertheless, cooperation is widespread across biological and social systems, and many mechanisms have been proposed to explain why. Several of these, includ-

E-mail address: ebrush@umd.edu (E. Brush).

ing ostracism (Tavoni et al., 2012), punishment (Nowak, 2006), and reciprocity (Axelrod and Hamilton, 1981; Killingback and Doebeli, 2002; Nowak, 2006; Ohtsuki and Iwasa, 2006; Pacheco et al., 2006; Panchanathan and Boyd, 2003), rely on members of a group using information to discriminate in their behavior toward their peers. Such agents are called discriminators, as opposed to cooperators and defectors, who do not change their behaviors based on such information. But even among humans, individuals rarely—if ever have perfect and complete information about all members of their social groups. Nor do they observe and interact with their peers entirely randomly. It is therefore important to understand how assortment within groups and constraints on the available information impacts the evolution of cooperation.

A commonly considered strategy for discriminators to use the information they have about their peers is to behave reciprocally, being more likely to cooperate with agents whom they expect to cooperate. Direct reciprocity is possible when pairs of agents en-

 $<sup>^{\</sup>ast}$  Corresponding author at: Department of Biology, University of Maryland, College Park, MD 20742, USA

gage in repeated interactions (Axelrod and Hamilton, 1981; Killingback and Doebeli, 2002; Nowak, 2006), so that paired agents can base their future behaviors on the past behaviors of their partners that they have experienced directly. In contrast, reciprocity is indirect when discriminators use information about the interactions between other pairs of agents, rather than memories of their own interactions, to decide how to behave. Indirect reciprocity can explain the persistence of cooperation even in groups whose members are unlikely to repeatedly interact with each other, and has thus frequently been used to model the evolution of cooperation (e.g., Brandt and Sigmund, 2004; Brandt and Sigmund, 2006; Nakamura and Masuda, 2011; Nowak and Sigmund, 1998a,b; Ohtsuki and Iwasa, 2006; Pacheco et al., 2006; Panchanathan and Boyd, 2003; Uchida, 2010; Uchida and Sigmund, 2010). (For discussions of direct reciprocity, see e.g., Killingback and Doebeli, 2002 and Nowak, 2006.)

Many existing models assume that there is no group structure, so that each agent is equally likely to encounter every other. However, few-if any-real biological groups are perfectly well-mixed. If members of a group inherit their behavioral strategies from their parents and do not move far from where they are born, the group will comprise patches of agents with similar behaviors. Structure can also arise if members of a group move away from agents who have defected against them (Hamilton and Taborsky, 2005) or away from parts of the environment that have been depleted by defectors (Pepper and Smuts, 2002). Each of these mechanisms could lead to different frequencies of interacting with cooperators, defectors, and discriminators, resulting in what we call interaction assortment. Positive interaction assortment has been shown to be effective for promoting cooperation (e.g., Ackermann et al., 2008; Axelrod and Hamilton, 1981; Doebeli and Hauert, 2005; Fletcher and Doebeli, 2006; Ghang and Nowak, 2015; Panchanathan and Boyd, 2004; Pepper and Smuts, 2002; Rankin and Taborsky, 2009; Roberts, 2015; for an exception see Hauert and Doebeli, 2004), while negative interaction assortment tends to inhibit cooperation (Fletcher and Doebeli, 2006; Forber and Smead, 2014; Smead and Forber, 2013; West and Gardner, 2010).

Any mechanism that leads to interaction assortment could also lead to different frequencies of observing cooperators, defectors, and discriminators, resulting in what we call information assortment, which has not previously been studied. Furthermore, only a handful of studies have considered limited information, and these studies do not explicitly model the process of information gathering and storing (e.g. Brandt and Sigmund, 2006; Kreps et al., 1982; Nakamura and Masuda, 2011; Nowak and Sigmund, 1998a,b; Panchanathan and Boyd, 2003). With the exception of Kreps et al. (1982), who assumed that co-players do not always select the most rational strategy among those available to them, the few studies that considered indirect reciprocity under limited information assumed that each discriminator knows the last action of a fraction of its group at each point in time (e.g. Nakamura and Masuda, 2011; Nowak and Sigmund, 1998a,b; Panchanathan and Boyd, 2003). Limited information is thus described only phenomenologically, since the process by which discriminators collect such information is not considered. These earlier descriptions are also memory-less, since only behaviors at the last point in time is allowed to affect the discriminators' assessments and resultant behaviors. Finally, most models of indirect reciprocity ignore the costs incurred by discriminators for their information-related behaviors (but see Brandt and Sigmund, 2006). In reality, however, gathering and storing information can be costly, since it takes time and energy to engage in those activities, as has been studied in ecology, animal behavior, economics, and neuroscience (Laughlin, 2001; Laughlin et al., 1998; MacIver et al., 2010; Nelson, 1970; Waddington, 1985).

In this paper, we investigate how interaction assortment, information assortment, limited information, and costly information affect the ability of discriminators to stabilize cooperation. To study the dynamics of a group consisting of cooperators, defectors, and discriminators using indirect reciprocity, we extend the influential model of Nowak and Sigmund (1998b). In this model, three types of agents-cooperators, defectors, and discriminators-interact with each other for several rounds, during which discriminators cooperate with other agents that have recently cooperated and defect otherwise. We incorporate interaction assortment by allowing each type of agent to interact more or less frequently with other agents of the same type, and we incorporate information assortment by allowing discriminators to observe other discriminators more or less frequently than they observe the other types. Additionally, we incorporate limited information by restricting the number of observations that discriminators can make and by allowing discriminators to forget their observations of behaviors occurring more than one time step ago. Finally, we impose costs on the discriminators for their information-related behavior.

We find that cooperation can be stabilized by the presence of discriminators, provided that the discriminators preferentially interact with other types of agents or preferentially observe other discriminators, even when the discriminators have limited information. Surprisingly, making more information available to discriminators sometimes makes it harder for them to protect a cooperative group from invasion by defectors. Finally, we find that it becomes more difficult for discriminators to stabilize cooperation if they have to pay costs for gathering and storing information.

#### 2. Model description

We model a group of agents who cooperate to differing extents: cooperators always cooperate, defectors never cooperate, and discriminators use information about their peers to decide whether to cooperate or to defect. All agents interact with each other and receive payoffs according to their own behavior and the behaviors of the agents they interact with. These payoffs then determine how the frequencies of the three types of agents change over time, with agents that receive higher payoffs becoming more frequent. In the following sections, we describe the agents and how they interact; how discriminators gather, store, and use information; how the expected payoff for each type of agent is calculated; and how these payoffs affect the frequencies of the types of agents.

#### 2.1. Interaction dynamics

Following Nowak and Sigmund (1998b), we model cooperative interactions using the donation game. When two agents interact, each agent in the pair is given the opportunity to donate to its partner. If he chooses to donate, the recipient receives a benefit *b* and the donor incurs a cost *c*. If he chooses not to donate, neither agent's payoff changes. There are three types of agents. Cooperators always donate, defectors never donate, and discriminators decide whether or not to donate based on what they know about the recipient. We denote the frequency of cooperators in the group by  $x_1$ , that of defectors by  $x_2$ , and that of discriminators by  $x_3$ . We model a group that is sufficiently large (or in mathematical terms, infinitely large) that these quantities can take any value between 0 and 1. The set of combinations ( $x_1$ ,  $x_2$ ,  $x_3$ ) with  $x_1$ ,  $x_2$ ,  $x_3 \ge 0$  and  $x_1 + x_2 + x_3 = 1$  is called the two-dimensional simplex.

The agents play the game for *R* rounds. Agents can be more or less likely to interact with other agents of the same type than with other types, or equally likely to interact with all types, depending on the assumed degree of what we call interaction assortment. Specifically, we assume that an agent is more likely by a factor  $a_{int}$  to interact with another agent of the same type than with either

one of the other two types. For example, given that a discriminator engages in an interaction, he interacts with a cooperator with probability  $x_1/(x_1 + x_2 + a_{int}x_3)$ , with a defector with probability  $x_2/(x_1 + x_2 + a_{int}x_3)$ , or with another discriminator with probability  $a_{int}x_3/(x_1 + x_2 + a_{int}x_3)$ . Interaction probabilities for the other two types are defined analogously. When  $a_{int} = 1$ , the group is well mixed with regard to interactions, so any agent interacts with each of the three types with probabilities equaling their frequencies in the group. When  $a_{int} > 1$ , the group is positively assorted with regard to interactions, with agents being more likely to interact with agents of the same type, whereas when  $a_{int} < 1$ , the group is negatively assorted with regard to interactions, with agents being more likely to interact with agents of different types.

#### 2.2. Information dynamics

Discriminators observe other agents' behaviors and use those observations to update their opinions about the reputations of those other agents. Discriminators can be more, less, or equally likely to observe discriminators as other types, depending on the assumed degree of what we call information assortment. Specifically, a discriminator is more likely by a factor  $a_{inf}$  to observe another discriminator than either of the other two interaction types. In each round of the game, a discriminator makes several observations. For each observation, he chooses to observe a cooperator with probability  $x_1/(x_1 + x_2 + a_{inf}x_3)$ , a defector with probability  $x_2/(x_1 + x_2 + a_{inf}x_3)$ , and a discriminator with probability  $a_{inf}x_3/(x_1 + x_2 + a_{inf}x_3)$ . In total, a discriminator observes a fraction  $p_0$  of all agents in the group. As fractions of the group,  $p_0 x_1/(x_1 + x_2 + a_{inf} x_3)$  are cooperators that are observed by a focal discriminator,  $p_0 x_2/(x_1 + x_2 + a_{inf}x_3)$  are observed defectors,  $p_0 a_{inf} x_3 / (x_1 + x_2 + a_{inf} x_3)$  are observed discriminators, and  $1 - p_0$ go unobserved.

Note that the fraction of agents a discriminator can observe depends on the information assortment: if there are very few discriminators present in the group and a discriminator concentrates its observations on those few discriminators ( $a_{inf} >> 1$ ), he can observe only a small fraction of the group. Similarly, if the group comprises mostly discriminators and a discriminator concentrates its observations on cooperators and defectors ( $a_{inf} \ll 1$ ), he can only observe a small fraction of the group. To ensure that discriminators can observe their peers with probability  $p_0$  for all group compositions, i.e., for all values of  $x_1$ ,  $x_2$ , and  $x_3$ , we therefore require  $p_0 \le \min\{a_{\inf}, 1/a_{\inf}\}$ . Details on deriving these bounds on  $p_0$ are described in the Supporting Information, Section S1. Based on these considerations, one might expect that  $a_{int}$  would constrain interactions in a similar way. However, each agent interacts with only one other agent in a given round, and in an infinitely large group one agent merely constitutes an infinitesimal proportion of the whole group. Thus, the "probability of interacting" is essentially 0, which is always less than or equal to  $min\{a_{int}, 1/a_{int}\}$ , and the required degree of interaction assortment can therefore always be achieved.

After each round, a discriminator classifies every other agent as good, bad, or unknown. When a discriminator has observed another agent cooperating, he updates his opinion of that agent to be good (i.e., to have a good reputation), and when a discriminator has observed another agent defecting he updates his opinion of that agent to be bad (i.e., to have a bad reputation), which is the image-scoring method of reputation updating used by Nowak and Sigmund (1998b). If a discriminator has never observed the other agent, he considers him to be unknown. Moreover, to describe the effects of memory loss on reputation information, each agent that is known to a discriminator at time t - 1 is independently remembered with probability  $p_r$  and becomes unknown with probability  $1 - p_r$  at time t. In the Supporting Information, Section S2, we de-

rive expressions for the probability of being known to a discriminator and for the probability that a discriminator is considered to be good.

As in the model of Nowak and Sigmund (1998b), a discriminator cooperates with any agent he considers to be good, defects against any agent he considers to be bad, and cooperates with probability  $p_c$  with unknown agents. In the case of perfect information, Brandt and Sigmund (2004) call this the "CO action rule", since it relies only on the reputation of a discriminator's co-player. For our analyses, we use  $p_c = 0.5$ . If the interaction and assortment parameters allow for the existence of a stable cooperative equilibrium when  $p_c = 0.5$ , it will also exist for a wide range of values of  $p_c$  less than 1. In the extreme case described by  $p_c = 1$ , there will not be a unique cooperative equilibrium, but discriminators can still prevent the invasion of defectors, so our conclusions for  $p_c = 0.5$  carry over even to this extreme case. We provide further details about the sensitivity of our model to this parameter in Section 3.5 and in the Supporting Information, Section S4 and Figs. S4-S7.

In previous models of indirect reciprocity (e.g., Brandt and Sigmund, 2004; Brandt and Sigmund, 2006; Panchanathan and Boyd, 2003), discriminators sometimes committed "errors," whereby a discriminator either does not cooperate when intending to do so (implementation error) or does not correctly perceive a partner's reputation (assessment error). In either case, a discriminator may defect against a cooperator. In our model, this possibility is incorporated through limited information: if a cooperator is unknown to a discriminator, the discriminator may defect against it. We do not separately incorporate errors into our model in order to keep a clear focus on the effects of limited information, without having to disentangle them from the effects of errors. While the possibility of a discriminator committing an error can undermine the stability of cooperation under indirect reciprocity (Panchanathan and Boyd, 2003), it does not always do so (Brandt and Sigmund, 2004; 2006). Similarly, we find that limited information can destabilize cooperation, but that the limits on information have to be severe to do so, as we show below.

To impose costs on discriminators for gathering and storing information, a cost  $s \ge 0$  is deducted, once at the end of the *R* rounds of interactions, from the payoff a discriminator has accrued from those interactions.

#### 2.3. Payoff dynamics

The expected payoffs for each of the three types depend on the frequency  $x_1$  of cooperators, the frequency  $x_2$  of defectors, and the frequency  $x_3$  of discriminators. Since the discriminators' behaviors depend on their opinions about other agents, an agent's expected payoff also depends on the probability that a discriminator will have an opinion about him or her. When a discriminator has an opinion, he will always assess a cooperator as good and a defector as bad. The probability that a discriminator has a good opinion about another discriminator thus depends on the behaviors observed by the discriminator, and hence on the frequencies of the three types. In general, the expected payoff of an agent is

$$P = b \sum_{t=1}^{R} (\text{probability that the agent receives a donation at time } t)$$
$$-c \sum_{t=1}^{R} (\text{probability that the gives a donation at time } t).$$

We derive expressions for the expected payoffs of each type of agent in the Supporting Information, Section S3.

#### 2.4. Replicator dynamics

We are interested in the dynamics of the frequencies of the three types,  $x_1$ ,  $x_2$ , and  $x_3$ . These dynamics are given by the standard replicator equations,  $\frac{d}{dt}x_i = x_i(P_i - \bar{P})$ , where  $\bar{P} = \sum_i x_i P_i$  is the average payoff in the group. Hence, the frequencies of types are equilibrated when, for each type *i*, either  $x_i = 0$  or  $P_i = \bar{P}$ .

#### 3. Results

The replicator dynamics resulting from our model can reach seven types of equilibria. There are always three pure equilibria, at which the group consists entirely of one type of agent. The pure cooperator equilibrium is always unstable. The pure defector equilibrium is always stable. The pure discriminator equilibrium is always a saddle: either a group of discriminators can be invaded by cooperators, but not by defectors, or a group of discriminators can be invaded by defectors, but not by cooperators, depending on the parameters of the model. There are also four possible "mixed" equilibria: three of these correspond to groups that consist of two types of agents, and one is an "interior" equilibrium, corresponding to a group in which all three types of agents are present. The cooperator-discriminator equilibrium, when it exists, is maintained by mutual invasibility and is always stable along the cooperatordiscriminator edge of the simplex: in a group mostly made up of discriminators, cooperators receive more benefits than discriminators, who might be perceived as bad by their peers, while in a group mostly made up of cooperators, discriminators pay lower costs than cooperators, who always donate. The existence and stability of the cooperative equilibria, that is, equilibria in which cooperators are present, depend on how assorted the group is, how the discriminators gather and store information, and how large the costs associated with these behaviors are. By analyzing how the replicator dynamics depend on these factors, we find that (1) cooperation is stabilized when the group has negative interaction assortment or positive information assortment or both, even if the discriminators have limited information; (2) increasing the probabilities of observing and/or remembering can help defectors invade, and (3) costly information can jeopardize cooperation. We now describe each of these findings in turn.

#### 3.1. Assortment can stabilize cooperation

If there is no assortment ( $a_{inf} = a_{int} = 1$ ), defection will always come to dominate the group. When the group starts with a sufficient fraction of discriminators, it will come to cycle around a neutral interior equilibrium: discriminators first increase at the expense of defectors, then cooperators increase at the expense of discriminators, and then defectors increase by taking advantage of cooperators, and the cycle continues (Fig. 1D). However, if there is a big enough perturbation, the group can be moved into a regime where defection takes over (Fig. 1D) (Nowak and Sigmund, 1998b). In the Supporting Information, Fig. S1, we show that the neutral interior equilibrium is the only possible mixed equilibrium when  $a_{inf} = a_{int} = 1$ , regardless of how much information the discriminators have. If the discriminators do not have sufficient information, even this interior equilibrium does not exist and no perturbation is required for defectors to take over (Supporting Information, Fig. S1).

With sufficient positive interaction assortment (i.e., far enough to the right to be in the purple region of Fig. 1A), a stable and an unstable cooperator-defector equilibrium appear together (as can be seen in the transition from Fig. 1D to F). Defectors can always invade the pure cooperator equilibrium, since they accrue higher payoffs than cooperators: as long as defectors are rare, both types essentially interact only with cooperators, but defectors save the cost of cooperating. However, when a significant fraction of the group consist of defectors, a cooperator receives a higher payoff than a defector, because the cooperator frequently interacts with other cooperators, offsetting the costs he has to pay for cooperating, while the defector frequently interacts with other defectors. These forces are balanced at the two cooperator-defector equilibria.

Positive interaction assortment cannot stabilize the cooperatordiscriminator equilibrium. Rather, this can be achieved by *reducing* interaction assortment or increasing information assortment. Reducing interaction assortment results in a stable interior equilibrium at which all three types are present (as seen in the transition from Fig. 1D to C). As  $a_{int}$  is reduced further, more and more discriminators can invade a group starting from the pure cooperator equilibrium, since the discriminators are receiving higher and higher payoffs from frequently interacting with cooperators. Eventually, the frequency of discriminators at the cooperatordiscriminator equilibrium is high enough that the discriminators can prevent defectors from invading and the equilibrium is stabilized (as seen in the transition from Fig. 1C to B).

As information assortment increases, discriminators know more about other discriminators than about cooperators and therefore give more donations to discriminators and fewer to cooperators. This increases the payoffs that discriminators receive in the absence of defectors, allowing more discriminators to invade the pure cooperator equilibrium, to the point until there are enough discriminators to prevent defectors from invading (as seen in the transition form Fig. 1D to E). Details about these bifurcations are provided in the Supporting Information, Section S5. If we only consider situations in which the two types of assortment are equal, they both need to be negative in order for cooperation to be stabilized (as seen by moving along the dashed diagonal line in Fig. 1).

The degree of either interaction assortment or information assortment required to stabilize the cooperator-discriminator equilibrium (which can be seen in the distance between the point D and the dark-blue region in Fig. 1A) decreases as the number *R* of rounds increases, and in the limit of infinitely many rounds no assortment is required to stabilize this equilibrium (Supporting Information, Fig. S2). The robustness of these results to changing the probability  $p_c$  of cooperating and the benefit *b* of receiving a donation are discussed below, in Section 3.5.

#### 3.2. Even limited information can stabilize cooperation

For discriminators to operate and to be able to stabilize cooperation, the probabilities  $p_0$  of observing and  $p_r$  of remembering both need to exceed 0 (Fig. 2A). Increasing  $p_0$  and  $p_r$  from 0 decreases the benefits defectors receive from discriminators to whom they are unknown. When  $p_0$  and  $p_r$  are sufficiently high, a stable cooperator-discriminator equilibrium appears (as seen in the transition from Fig. 2B to C). Details about these bifurcations are provided in the Supporting Information, Section S5.

For a stable equilibrium to exist at which cooperators are present, the probabilities  $p_0$  and  $p_r$  need not be very high, and the higher the one the lower the other may be (see the boundary between the red and dark-blue regions in Fig. 2A). Thus, even limited information can stabilize cooperation. In fact, the more rounds the group plays and the greater the benefit of cooperation, the less information is needed to stabilize cooperation (Supporting Information, Figure S3).

# 3.3. Increasing the probabilities of observing or remembering can help defectors invade

Surprisingly, if the probabilities  $p_0$  of observing and  $p_r$  of remembering are low but sufficient to stabilize the cooperatordiscriminator equilibrium, increasing them further can allow de-



**Fig. 1.** Assortment, either in information or in interaction, is necessary, but not sufficient, to stabilize cooperation. In the upper panel (A), we show how the replicator dynamics depend on the degrees of information assortment  $a_{inf}$  and interaction assortment  $a_{int}$ . The axes are scaled logarithmically. The dashed line shows where  $a_{inf} = a_{int}$ . The parameter space is colored according to the most cooperative outcome of the replicator dynamics that occurs for a given combination of these parameters. A group made up entirely of defectors is always at a stable equilibrium. In the white region, it is the only stable equilibrium at which all three types are present. In the purple region, there is a stable cooperator-discriminator equilibrium. In the light-blue region, there is a stable cooperator, defectors equilibrium. In the parameter (B)-(F), trajectories show how the frequencies of cooperators, defectors, and discriminators change over time. The lower left corner of the simplex represents a group made up entirely of cooperators, the lower right corner a group made up entirely of defectors, and the upper corner a group made up entirely of discriminators. The colors in the simplices indicate the basins of attraction of the stable equilibria or a region in which trajectories cycle around a neutral center. Unstable equilibria are indicated with white circles, stable equilibria with black circles, stadles with half white and half black circles, and neutral centers with gray circles. Parameters: in B,  $a_{int} = 0.93$ ,  $a_{inf} = 0.93$ ; in C,  $a_{int} = 0.98$ ,  $i_{inf} = 0.98$ ; in D,  $a_{int} = 1.05$ ,  $a_{inf} = 1.17$ ; in E,  $a_{int} = 1.005$ ,  $a_{inf} = 1.17$ ; in F,  $a_{int} = 1.24$ ,  $a_{inf} = 1.17$ ; in all panels,  $p_0 = 0.85$ ,  $p_r = 0.95$ , R = 10, b = 10, c = 1,  $p_c = 0.5$ , and s = 0. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

fectors to invade and coexist with cooperators and discriminators at a stable interior equilibrium (as seen in the transition from Fig. 2C to D and in Fig. 3A and C). From there, a stable cooperatordiscriminator equilibrium can be recovered by increasing  $p_0$  further until the stable interior equilibrium disappears, as seen in Figs. 2A and 3A. As the interior equilibrium appears, the probability of any type of agent receiving a donation decreases because of the presence of defectors (Fig. 3B and D). In other words, making more observations can sometimes undermine cooperation. At first sight unexpected, we can explain this finding as follows.

Whether defectors can invade the cooperator-discriminator equilibrium is affected by the balance between the advantage to cooperators from being known by discriminators and the advantage to defectors from a high frequency of cooperators. As either  $p_0$ or  $p_r$  increase, more cooperators can invade a group starting from the pure discriminator equilibrium, since they benefit from being known to discriminators and since they receive higher payoffs than discriminators, who sometimes defect (Fig. 3A and C). Once the fraction of discriminators at the cooperator-discriminator equilibrium is low enough, defectors can invade and exploit the cooperators (Fig. 3A and C). As the probability of observing is increased further, the information acquired by discriminators allows them to cooperate selectively with cooperators while defecting against defectors. The frequency of defectors then decreases until they are eliminated altogether, resulting in a stable mixture of cooperators and discriminators (Fig. 3A).

These considerations also explain why cooperation can be stabilized by information assortment (Fig. 1A). Increasing information assortment decreases the information discriminators have about the other types. Again, this reduces the frequency of cooperators, which are readily exploited by defectors, and thus ultimately reduces the frequency of defectors. The robustness of these results to changing the values of the probability  $p_c$  of cooperating and to the benefit *b* of receiving a donation are discussed below, in Section 3.5.

#### 3.4. Costly information can jeopardize cooperation

Without a cost for information gathering or storage (cost of information, for short), sufficient assortment and sufficient observation can stabilize the cooperator-discriminator equilibrium. Making information costly can destabilize this equilibrium (Fig. 4), which can be understood as follows.

When the cost of information is increased, there are more cooperators at the cooperator-discriminator equilibrium, because the discriminators are disadvantaged by paying a higher cost of information. This allows defectors to invade and coexist with cooperators and discriminators at a stable interior equilibrium (as seen in the transition from Fig. 4B to C). As the cost of information is increased further, the discriminators eventually do so poorly as to be unable to prevent defectors from dominating the group (as seen in the transition from Fig. 4C to D).

As we have seen above, in the absence of costs, increasing the probabilities  $p_0$  of observing or  $p_r$  of remembering can make it easier for defectors to invade. This shifts the group composition from a stable equilibrium with only cooperators and discrimina-



**Fig. 2.** Even limited information can stabilize cooperation. In the upper panel (A), we show how the replicator dynamics depend on the two characteristics of the process of information gathering and storing, given by the probabilities  $p_0$  of observing and  $p_r$  of remembering. The horizontal axis extends until  $p_0 = a_{inf}$ , beyond which  $p_0$  is not meaningful (see the Supporting Information, Section S1). The parameter space is colored according to the most cooperative outcome of the replicator dynamics that occurs for a given combination of these parameters. A group made up entirely of defectors is always at a stable equilibrium. In the red region, it is the only stable equilibrium. In the dark-blue region, there is a stable cooperator-discriminator equilibrium. In the light-blue region, there is a stable cooperator, the lower right corner a group made up entirely of defectors, and discriminators change over time. The lower left corner of the simplex represents a group made up entirely of the stable equilibria up entirely of defectors, the upper corner a group made up entirely of discriminators. The colors in the simplices indicate the basins of attraction of the stable equilibria. Unstable equilibria are indicated with white circles, stable equilibria with black circles,  $n_0 = 0.3$ ; in D,  $p_r = 1$ ,  $p_0 = 0.3$ ; in all panels,  $a_{int} = a_{inf} = 0.93$ , R = 10, b = 10, c = 1,  $p_c = 0.5$ , and s = 0. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 3.** Increasing the probabilities  $p_0$  of observing or  $p_r$  of remembering can allow defectors to invade and decrease the probability of cooperation. In (A) and (B), we show the frequencies of all three types of agents, first at the stable cooperator-discriminator equilibrium and then at the stable interior equilibrium that the former turns into, as functions of the probabilities  $p_0$  and  $p_r$ , respectively. This is equivalent to taking a horizontal and a vertical path, respectively, through Fig. 2A. In (C) and (D), we show the probability of each type of agent receiving a donation across games played with random partners, first at the stable cooperator-discriminator equilibrium and then at the stable interior equilibrium that the former turns into, as functions of the probabilities  $p_0$  and  $p_r$ , respectively. In each panel, the blue curve refers to cooperators, the red curve to defectors, and the green curve to discriminators. If no curves are shown for a particular value of  $p_0$  or  $p_r$ , no stable cooperative equilibrium exists for that value. Parameters:  $p_r = 1$  (unless varied),  $p_0 = 0.3$  (unless varied),  $a_{int} = a_{inf} = 0.93$ , R = 10, c = 1,  $p_c = 0.5$ , and s = 0. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 4.** Costly information can destabilize cooperation. Moreover, when information is costly, increasing the probability of observing can also destabilize otherwise stable cooperation. In the upper panel (A), we show how the replicator dynamics depend on the probability  $p_o$  of observation and the cost *s* of information. The horizontal axis is scaled logarithmically and extends until  $p_o = a_{inf}$ , beyond which  $p_o$  is not meaningful (see Supporting Information, Section S1). The parameter space is colored according to the most cooperative outcome of the replicator dynamics that occurs for a given combination of these parameters. A group made up entirely of defectors is always at a stable equilibrium. In the red region, it is the only stable equilibrium. In the dark-blue region, there is a stable cooperator-discriminator equilibrium. In the light-blue region, there is a stable equilibrium at which all three types are present. In the phase portraits (B)-(D), trajectories show how the frequencies of cooperators, defectors, and discriminators change over time. The lower left corner of the simplex represents a group made up entirely of cooperators, the lower right corner a group made up entirely of defectors, and the upper corner a group made up entirely of discriminators. The colors in the simplices indicate the basins of attraction of the stable equilibria with black circles, and saddles with half white and half black circles. Parameters: in B, s = 0.005; in C, s = 0.035; in D, s = 0.065; in all panels,  $p_o = 0.8$ ,  $p_r = 0.9$ ,  $a_{int} = a_{inf} = 1.01$ , R = 10, b = 10, c = 1, and  $p_c = 0.5$ . (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

tors to a stable interior equilibrium at which defectors are also present. A stable cooperator-discriminator equilibrium can then be recovered by increasing  $p_0$  further. When information is sufficiently costly, increasing the probability of observing can no longer stabilize the cooperator-discriminator equilibrium and only serves to destabilize the stable interior equilibrium, causing defectors to dominate the group (as seen in the transition from Fig. 4C to D). Details about these bifurcations are provided in the Supporting Information, Section S5.

#### 3.5. Robustness

For the analyses above, the probability  $p_c$  that a discriminator donates to an unknown agent is set to 0.5. Our results are robust to changing this value. To see this, we recall that there are three types of stable equilibria at which cooperators are present: a stable cooperator-defector equilibrium, a stable cooperator-discriminator equilibrium, and a stable interior equilibrium. Since discriminators are not present at a stable cooperator-defector equilibrium and  $p_c$ only affects how discriminators behave toward unknown agents,  $p_c$  does not affect the existence or stability of such an equilibrium (Supporting Information, Figs. S4-S7). If a stable cooperatordiscriminator equilibrium exists when  $p_c = 0.5$ , it will exist also for all values  $p_c < 1$ , assuming that s = 0 (as seen in the Supporting Information, Section S4 and Figs. S4-7). In other words, parameter combinations  $a_{int}$ ,  $a_{inf}$ ,  $p_o$ , and  $p_r$  that give rise to a stable cooperator-discriminator for  $p_c = 0.5$  do the same for all values of  $p_{\rm c}$  < 1, so the boundaries of the dark-blue regions in Figs. 1 and 2 do not change as  $p_c$  is varied. If a stable interior equilibrium exists when  $p_c = 0.5$ , it will exist also for all values  $0.5 < p_c < 1$  (as seen in the Supporting Information, Figs. S4 and S6), as well as for values of  $p_c$  as low as 0.1, depending on the other parameters (as seen in the Supporting Information, Figs. S5 and S7). In other words, parameter combinations  $a_{int}$ ,  $a_{inf}$ ,  $p_0$ , and  $p_r$  that give rise to a stable interior equilibrium for  $p_c = 0.5$  do the same for a wide range of values of  $p_c$ . For  $p_c = 1$ , the edge of the simplex containing mixtures of cooperators and discriminators becomes a line of equilibria that are neutral along that line. If there is either a stable cooperator-discriminator equilibrium or a stable interior equilibrium for  $p_c$  just less than 1, any trajectory that starts with sufficiently many discriminators will move toward this edge (as seen in the Supporting Information, Figs. S4 and S6), so it can still be said that discriminators can keep defectors at bay (more details are provided in the Supplementary Information, Section S4). If a neutral interior equilibrium exists for  $p_c = 0.5$ , changing  $p_c$  can either stabilize or destabilize this equilibrium, depending on whether  $p_{\rm c}$ increases or decreases and on whether  $a_{int}$  is greater than or less than 1 (as seen in the Supporting Information, Section S4 and Figs. S4 and S5).

For the analyses above, the benefit b from receiving a donation is set to 10. We show in the Supporting Information, Figure S8, that our findings about the effects of both interaction assortment and information assortment remain qualitatively unchanged at smaller values of b. We also show in the Supporting Information, Figure S8, that our findings that only moderate amounts of information are required to stabilize cooperation and that increasing information too much can jeopardize cooperation remain qualitatively unchanged at smaller values of *b*. One change brought about by reducing *b* is that too much information can be even more disastrous for cooperation: now increasing either  $p_r$  or  $p_0$  can turn a stable interior equilibrium into a neutral center. This is indicated by the white regions in the Supporting Information, Figure S8B,D.

#### 4. Discussion

We set out to answer the question of whether discriminators with limited information can promote and maintain cooperation and, if so, under what conditions. These questions have previously been addressed, but earlier models often made unrealistic assumptions about the discriminators abilities and behaviors. Here we have introduced and analyzed a model that is more realistic in that there is assortment in the groups interactions, there is assortment in how discriminators observe the rest of the group, discriminators have limited amounts of information, and discriminators must pay costs for gathering or storing information. On this basis, we find that when interactions are negatively assorted or observations are positively assorted, discriminators can eliminate defectors from the group. We also find that even with limited information discriminators can prevent the invasion of defectors and that increasing the information they have about their peers can impede their ability to do so. Finally, we find that when information gathering or storing is costlier, discriminators are less able to stabilize cooperation.

If only cooperators and defectors are present, sufficient positive interaction assortment can allow a group to reach a stable mix of both types. This finding is in agreement with previous work showing that interaction assortment can stabilize cooperation when cooperators are more likely to interact with other cooperators than with defectors (Ackermann et al., 2008; Axelrod and Hamilton, 1981; Doebeli and Hauert, 2005; Fletcher and Doebeli, 2006; Ghang and Nowak, 2015; Nowak, 2006; Panchanathan and Boyd, 2004; Pepper and Smuts, 2002; Rankin and Taborsky, 2009; Roberts, 2015). Through the presence of discriminators, who use indirect reciprocity to decide how to behave, a group can reach an equilibrium at which both cooperators and discriminators, and sometimes only cooperators and discriminators, are present. This finding agrees with previous models in which the presence of discriminators using indirect reciprocity to decide when to cooperate helped support cooperation (Brandt and Sigmund, 2006; Nakamura and Masuda, 2011; Nowak and Sigmund, 1998a,b; Ohtsuki and Iwasa, 2006; Panchanathan and Boyd, 2004; Uchida and Sigmund, 2010). In particular, our model reverts to that of Nowak and Sigmund (1998b) and recovers their results when we consider discriminators with no assortment, full information about their peers, and cost-free gathering and storing of information.

When all three types of agents are present, negative interaction assortment allows a mix of cooperators and discriminators to become stable against invasion by defectors. This is in stark contrast to most previous studies of negative interaction assortment. For example, negative assortment has been found to impede the evolution of cooperation (Fletcher and Doebeli, 2006) and to support the evolution of spite, an action that hurts both the actor and the recipient (Forber and Smead, 2014; Smead and Forber, 2013; West and Gardner, 2010). Negative assortment can also lead to a higher rate of conflict (Choi and Bowles, 2007). These undesirable consequences of negative interaction assortment occur in groups that consist only of a cooperating type and a defecting type. In that case, under negative interaction assortment, an agent of the defecting type receives a higher payoff from more frequently interacting with cooperators, raising the rate at which defection increases in frequency. In contrast, when discriminators are also present and all

three types interact with negative assortment, discriminators benefit from interacting more frequently with cooperators and can thus increase in frequency to such an extent that they are able to deny benefits to defectors. Our finding therefore broadens the set of circumstances that promote cooperation to include negative as well as positive interaction assortment.

Information assortment is a fundamentally new form of assortment, which we find to be beneficial for cooperation. Despite the large literature on the effects of interaction assortment on the evolution of cooperation, no other studies, to our knowledge, have considered the effects of information assortment. By examining how assortment might affect observations as well as interactions, we find a new way in which group structure can promote cooperation.

Assortment can arise through several mechanisms. If agents can recognize others of the same type, they could preferentially interact with or cooperate with them. This so-called "greenbeard mechanism is known to give rise to positive assortment (Gardner and West, 2010; Nonacs, 2011) and to support cooperation (Gardner and West, 2010; Nowak, 2006; Rankin and Taborsky, 2009; Sinervo et al., 2006; Smukalla et al., 2008). If agents recognize others of the same type and decide to avoid them, this will give rise to negative assortment. However, such a cognitive mechanism is not required for assortment to occur. If cooperative behavior has a genetic component and agents often interact with kin, a group will be positively assorted (Fletcher and Doebeli, 2006; Nowak, 2006; Panchanathan and Boyd, 2004). If, instead, offspring disperse away from their parents, a group may become negatively assorted. In models with only cooperators and defectors, both positive and negative assortment resulted when agents moved away from parts of the environment where defectors had depleted resources (Pepper and Smuts, 2002). Extrapolating these findings, we could expect to find both positive and negative assortment among all three types under similar circumstances. Finally, when animals inherit the social connections of their parents, the resulting social network is positively assorted, such that animals are more likely to be connected to others with traits similar to their own (Ilany and Akcay, 2016). Conversely, if they set out on their own to forge different relationships from their parents, we would expect the resulting social network to be negatively assorted.

In previous models, assortment only affected the rates at which different types of agents interact. In our model, it also affects the rates at which different types of agents are observed. It is likely that the two levels of assortment are equal in many situations. However, disentangling the two types of assortment allows us to study their respective effects. Additionally, if the two behaviors, interacting and observing, occur on different spatial and temporal scales, we expect the resulting assortments to be different. For instance, if agents can observe interactions occurring far away but only interact with others that are close to them, interaction assortment will exceed information assortment. Conversely, if cooperation can occur through acoustic or other long-range mechanisms and agents are in an environment where it is hard to see very far (e.g., birds in a dense forest or bats in a dark cave), information assortment will exceed interaction assortment. Even if we assume that the two assortment factors are equal (as we do in Figs. 2-4), we still find that varying assortment can result in the full range of possibilities from no stable cooperation, to a stable interior equilibrium, to a stable cooperative equilibrium (moving along the diagonal in Fig. 1).

In many realistic settings, there will be a complex interplay between density dependence, interaction assortment, and information assortment. For example, positive assortment among discriminators might mean that they are more densely packed and hence experience density-dependent birth and death rates differing from the other types of agents. We make the simplifying assumption that density dependence affects all agents equally. If assortment were to give rise to differential density dependence, we would expect that this would favor cooperators over defectors, assuming that cooperators improve the suitability of their environments while defectors deplete their surroundings. Thus, incorporating these effects into our model would tend to expand parameter combinations for which we find stable cooperation.

While limited information could be an obstacle to the emergence and maintenance of cooperation, we encouragingly find that, to promote cooperation, discriminators do not need to know about every agent in a group. In fact, even when the probabilities of observing other agents and of remembering those observations are low, a group can equilibrate with cooperators present. This result is encouraging for the stabilization of cooperation, since discriminators with more moderate information requirements pay less for their information gathering and storage and therefore are more likely to evolve. Cooperative groups less burdened by the costs of information can become more prosperous. Our results reinforce previous studies that find that discriminators with limited information can support cooperation (Brandt and Sigmund, 2006; Nakamura and Masuda, 2011; Nowak and Sigmund, 1998a,b). In particular, Nowak and Sigmund (1998b) analyzed limited information by assuming that, for any given discriminator, there is a fixed probability that he will know the reputation of any other agent. They further assumed that discriminators always donate to agents whose reputations they do not know (equivalent to setting our parameter  $p_c = 1$ ) and found that discriminators can stabilize cooperation if the probability of knowing about other agents exceeds a threshold. This is analogous to our finding that the probabilities of observing and remembering have to be sufficiently high for cooperation to be stabilized. In psychology and economics, it is increasingly recognized that humans have cognitive limitations that affect the level of optimality with which we can make decisions, as described by the theory of bounded rationality (Conlisk, 1996; Gigerenzer and Goldstein, 1996; Kahneman, 2003). Similarly, humans often choose to ignore some of the information available to them, a phenomenon known as rational inattention, which can affect, e.g., how consumers make decisions in economic models (Caplin and Dean, 2015; Matejka and Sims, 2011; Sims, 2003; 2006). It is therefore natural to consider agents with limited information and it is important to understand how this affects their behavior.

Surprisingly, increasing the ability of discriminators to observe their peers can help defectors, rather than cooperators. If discriminators do not yet observe other agents very frequently and start to increase their probability of making an observation, it becomes easier for defectors to invade the cooperative equilibrium. Increasing information only helps defectors invade when discriminators do not necessarily cooperate with strangers, as we show in the Supporting Information, Figure S6. This explains why previous studies of the effect of limited information on indirect reciprocity, such as Nowak and Sigmund (1998b), did not identify any negative effects of increased information. Studying a related model, Uchida (2010) also found that reducing the information players have about each other can make it easier for discriminators ("SCORING" agents in their terminology) to stabilize cooperation. In a similar spirit, Kreps et al. (1982) found that uncertainty about a partners rationality can help prevent defection. These effects can only be seen in models, like ours, that account for limited information.

Since the frequency of discriminators in the cooperatordiscriminator equilibrium increases as the discriminators have less information, if the discriminators abilities were evolving, either the probability of observing or that of remembering might decrease over time until they become too small to protect cooperators. This prediction is contingent, however, upon the assumption that discriminators only use a first-order assessment strategy, which does not depend on the reputation of the recipient. More sophisticated assessment rules and selection on the discriminators' processes of information gathering and storage are left for future work, as discussed below.

We have shown that imposing costs on the discriminators for gathering and storing information can jeopardize their limited ability to protect cooperation, which agrees with previous findings that information costs make it harder for indirect reciprocity to stabilize cooperation (Suzuki and Kimura, 2013). In our model, making information more costly can destabilize otherwise stable cooperative equilibria. There is also a counterintuitive interaction between costs and the probability of observing: when information is more costly, increasing the probability of observing can destabilize cooperation and enable defectors to dominate a group. It indeed seems likely that spending time and energy observing other agents and remembering those observations imposes some costs on discriminators (Caplin and Dean, 2015; Laughlin, 2001; Laughlin et al., 1998; Maclver et al., 2010; Nelson, 1970; Waddington, 1985), adding saliency to our corresponding findings.

In our model, discriminators use simple methods for assigning reputations to their peers. In particular, their opinions depend only on the last observation they can remember; they can categorize other agents only coarsely; and the way a donors reputation is updated does not depend on either his or the recipients reputations. As avenues for future research, it would be interesting to relax each of these three assumptions. In particular, other ways of assessing an agent's reputation can incorporate information about the reputations of both the focal agent and his interaction partner. For example, there are eight such assessment rules, the "leading eight," such that (1) if discriminators use these rules, a pure discriminator group is at a stable equilibrium, and (2) using these rules results in a high payoff for members of such a group (Ohtsuki and Iwasa, 2004; 2006). The mechanisms we consider here-interaction assortment, information assortment, and information gathering and storing-could be applied to groups with discriminators using these more complicated rules. An agents payoff in an assorted group using a more complicated assessment rule can no longer be derived analytically and will instead have to be computed numerically. Despite the complication of such a model, it would enable an interesting extension of our analyses. Since interaction assortment has been found to be important in many models, we expect that the benefits of information assortment will also generalize to other types of discriminators.

Moreover, the probabilities of observing and remembering, characterizing the discriminators' processes of information gathering and storing, are fixed in our model. In future work, it will be interesting to regard these characteristics as evolving traits that can differ among discriminators. The evolution of these traits can then be studied using adaptive-dynamics techniques. Related to this outlook, Kerr and Feldman (2003) analyzed a model in which agents gathered and stored information about their environment: they observed evolutionary branching through which a group could endogenously evolve two coexisting information-gathering strategies. It will be worthwhile exploring whether a similar kind of evolutionary branching can bring about a polymorphism of discriminators, in which, for example, some agents observe a lot, but have poor memory, while others make few observations, but remember those very well.

Our current work provides encouraging results about how cooperation can be maintained on the timescale of frequency changes among fixed types of agents, even by simple discriminators with limited information. The next big challenge is to understand the conditions under which discriminator-facilitated cooperation based on indirect reciprocity can be maintained when the behaviors of discriminators can evolve.

#### Acknowledgments

EB wishes to thank Simon Levin, Phil Holmes, Brian Fath, and Karl Sigmund for helpful discussions and the Young Scientists Summer Program at IIASA for a welcoming and productive environment in which to complete this work. EB acknowledges support during this project from a subaward from the Santa Fe Institute under a grant from the John Templeton Foundation for the study of complexity and from the training grant NIH 5T32HG003284. ÅB acknowledges financial support from the Swedish Research Council. UD acknowledges financial support by the European Commission, the European Science Foundation, the Austrian Science Fund, the Austrian Ministry of Science and Research, and the Vienna Science and Technology Fund.

#### Supplementary material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.jtbi.2018.01.005.

#### References

- Ackermann, M., Stecher, B., Freed, N.E., Songhet, P., Hardt, W.-D., Doebeli, M., 2008. Self-destructive cooperation mediated by phenotypic noise. Nature 454 (7207), 987–990.
- Axelrod, R., Hamilton, W.D., 1981. The evolution of cooperation. Science 211 (4489), 1390–1396.
- Brandt, H., Sigmund, K., 2004. The logic of reprobation: assessment and action rules for indirect reciprocation. J. Theor. Biol. 231 (4), 475–486.
- Brandt, H., Sigmund, K., 2006. The good, the bad and the discriminator-errors in direct and indirect reciprocity. J. Theor. Biol. 239 (2), 183-194.
- Caplin, A., Dean, M., 2015. Revealed preference, rational inattention, and costly information acquisition. Am. Econ. Rev. 105 (7), 2183–2203.
- Choi, J.-K., Bowles, S., 2007. The coevolution of parochial altruism and war. Science 318 (636), 636–640.
- Conlisk, J., 1996. Why bounded rationality? J. Econ. Lit. 34 (2), 669-700.
- Doebeli, M., Hauert, C., 2005. Models of cooperation based on the prisoner's dilemma and the snowdrift game. Ecol. Lett. 8 (7), 748–766.
- Fletcher, J.A., Doebeli, M., 2006. How altruism evolves: assortment and synergy. J. Evol. Biol. 19 (5), 1389–1393.
- Forber, P., Smead, R., 2014. The evolution of fairness through spite. Proc. R. Soc. B 281 (1780), 20132439.
- Gardner, A., West, S.A., 2010. Greenbeards. Evolution 64 (1), 25-38.
- Ghang, W., Nowak, M.A., 2015. Indirect reciprocity with optional interactions. J. Theor. Biol. 365, 1–11.
- Gigerenzer, G., Goldstein, D.G., 1996. Reasoning the fast and frugal way: models of bounded rationality. Psychol. Rev. 103 (4), 650–669.
- Hamilton, I.M., Taborsky, M., 2005. Contingent movement and cooperation evolve under generalized reciprocity. Proc. R. Soc. B 272, 2259–2267.
- Hauert, C., Doebeli, M., 2004. Spatial structure often inhibits the evolution of cooperation in the snowdrift game. Nature 428 (6983), 643–646.
- Ilany, A., Akcay, E., 2016. Social inheritance can explain the structure of animal social networks. Nat. Commun. 7. 12084 EP-
- Kahneman, D., 2003. Maps of bounded rationality: psychology for behavioral economics. Am. Econ. Rev. 93 (5), 1449–1475.
- Kerr, B., Feldman, M.W., 2003. Carving the cognitive niche: optimal learning strategies in homogeneous and heterogeneous environments. J. Theor. Biol. 220 (2), 169–188.
- Killingback, T., Doebeli, M., 2002. The continuous prisoner's dilemma and the evolution of cooperation through reciprocal altruism with variable investment. Am. Nat. 160 (4), 421–438.

- Kreps, D.M., Milgrom, P., Roberts, J., Wilson, R., 1982. Rational cooperation in the finitely repeated prisoner's dilemma. J. Econ. Theory 27 (2), 245–252.
- Laughlin, S.B., 2001. Energy as a constraint on the coding and processing of sensory information. Curr. Opin. Neurobiol. 11 (4), 475–480.
- Laughlin, S.B., de Ruyter van Steveninck, R.R., Anderson, J.C., 1998. The metabolic cost of neural information. Nat. Neurosci. 1 (1), 36–41.
- Maclver, M.A., Patankar, N.A., Shirgaonkar, A.A., 2010. Energy-information trade-offs between movement and sensing. PLoS Comp. Biol. 6 (5), e1000769.
- Matejka, F., Sims, C.A., 2011. Discrete actions in information-constrained tracking problems. CERGE-EI Working Paper Series 441.
- Nakamura, M., Masuda, N., 2011. Indirect reciprocity under incomplete observation. PLoS Comput. Biol. 7 (7), e1002113.
- Nelson, P., 1970. Information and consumer behavior. J. Polit. Econ. 78 (2), 311–329. Nonacs, P., 2011. Kinship, greenbeards, and runaway social selection in the evolution of social insect cooperation. Proc. Natl. Acad. Sci. U.S.A. 108 (Supplement 2), 10808–10815.
- Nowak, M., 2006. Five rules for the evolution of cooperation. Science 314 (5805), 1560–1563.
- Nowak, M., Sigmund, K., 1998a. Evolution of indirect reciprocity by image scoring. Nature 393 (6685), 573–577.
- Nowak, M.A., Sigmund, K., 1998b. The dynamics of indirect reciprocity. J. Theor. Biol. 194 (4), 561–574.
- Ohtsuki, H., Iwasa, Y., 2004. How should we define goodness?-reputation dynamics in indirect reciprocity. J. Theor. Biol. 231, 107–120.
- Ohtsuki, H., Iwasa, Y., 2006. The leading eight: social norms that can maintain cooperation by indirect reciprocity. J. Theor. Biol. 239 (4), 435–444.
- Pacheco, J.M., Santos, F.C., Chalub, F.A.C.C., 2006. Stern-judging: a simple, successful norm which promotes cooperation under indirect reciprocity. PLoS Comput. Biol. 2 (12), 1634–1638.
- Panchanathan, K., Boyd, R., 2003. A tale of two defectors: the importance of standing for evolution of indirect reciprocity. J. Theor. Biol. 224 (1), 115–126.
- Panchanathan, K., Boyd, R., 2004. Indirect reciprocity can stabilize cooperation without the second-order free rider problem. Nature 432 (7016), 499–502.
- Pepper, J.W., Smuts, B.B., 2002. A mechanism for the evolution of altruism among nonkin: positive assortment through environmental feedback. Am. Nat. 160 (2), 205–213.
- Rankin, D.J., Taborsky, M., 2009. Assortment and the evolution of generalized reciprocity. Evolution 63 (7), 1913–1922.
- Roberts, G., 2015. Partner choice drives the evolution of cooperation via indirect reciprocity. PLoS One 10 (6), e0129442.
- Sims, C.A., 2003. Implications of rational inattention. J. Monetary Econ. 50 (3), 665–690.
- Sims, C.A., 2006. Rational inattention: beyond the linear-quadratic case. Am. Econ. Rev. 96 (2), 158–163.
- Sinervo, B., Chaine, A., Clobert, J., Calsbeek, R., Hazard, L., Lancaster, L., McAdam, A.G., Alonzo, S., Corrigan, G., Hochberg, M.E., 2006. Self-recognition, color signals, and cycles of greenbeard mutualism and altruism. Proc. Natl. Acad. Sci. U.S.A. 103 (19), 7372–7377.
- Smead, R., Forber, P., 2013. The evolution dynamics of spite in finite population. Evolution 67 (3), 698–707.
- Smukalla, S., Caldara, M., Pochet, N., Beauvais, A., Guadagnini, S., Yan, C., Vinces, M.D., Jansen, A., Prevost, M.C., Latge, J.-P., Fink, G.R., Foster, K.R., Verstrepen, K.J., 2008. Flo1 is a variable green beard gene that drives biofilm-lik cooperation in budding yeast. Cell 135 (4), 736–737.
- Suzuki, S., Kimura, H., 2013. Indirect reciprocity is sensitive to costs of information transfer. Sci. Rep. 3.
- Tavoni, A., Schluter, M., Levin, S., 2012. The survival of the conformist: social pressure and renewable resource management. J. Theor. Biol. 299, 152–161.
- Uchida, S., 2010. Effect of private information on indirect reciprocity. Phys. Rev. E 82 (3), 036111.
- Uchida, S., Sigmund, K., 2010. The competition of assessment rules for indirect reciprocity. Proc. Natl. Acad. Sci. U.S.A. 263 (1), 13–19.
- Waddington, K.D., 1985. Cost-intake information used in foraging. J. Insect. Physiol. 31 (11), 891–897.
- West, S.A., Gardner, A., 2010. Altruism, spite, and greenbeards. Science 327 (5971), 1341–1344.

# Supporting information

### <sup>2</sup> S1 Attainable probabilities of observing

<sup>3</sup> Here we explain in greater detail why the probability  $p_0$  of observing is restricted not to <sup>4</sup> exceed min{ $a_{inf}$ ,  $1/a_{inf}$ }.

The intuitive explanation is as follows. If a discriminator focuses his observations 5 on other discriminators (i.e., if there is positive information assortment,  $a_{inf} > 1$ ), this 6 means that when a group contains only a few discriminators, the discriminator can 7 observe only a limited proportion of such a group. Similarly, if a discriminator focuses 8 his observations on other types of agents (i.e., if there is negative information assortment, 9  $a_{inf} < 1$ ), this means that when a group contains only a few cooperators and defectors, 10 the discriminator can observe only a limited proportion of such a group. Only when 11 the discriminators' observations are not assorted ( $a_{inf} = 1$ ) does it become possible for a 12 discriminator to observe the whole group ( $p_0 = 1$ ). 13

The mathematical explanation is as follows. Achieving the desired information assortment requires choosing a fraction  $p_0$  of the group in which the number of cooperators are proportional to  $x_1$ , of defectors to  $x_2$ , and of discriminators to  $a_{inf}x_3$ . Writing *C* for the positive proportionality constant, this is feasible if and only if

18  $Cx_1 \leq x_1,$ 19  $Cx_2 \leq x_2,$  and 20  $Ca_{\inf}x_3 \leq x_3.$ 

21

Hence,  $C \leq \min\{1, 1/a_{inf}\}$ . Since a discriminator observes a fraction  $p_0$  of the group, we

<sup>23</sup> must have  $p_0 = Cx_1 + Cx_2 + Ca_{inf}x_3$ . Thus,

$$p_{\rm o} \le x_1 + x_2 + a_{\rm inf} x_3$$
 and

25 26

These inequalities are fulfilled for all frequencies 
$$0 \le x_1, x_2, x_3 \le 1$$
 if and only if  $p_0 \le \min\{a_{inf}, 1/a_{inf}\}$ , as stated in the main text.

 $p_0 \leq x_1/a_{inf} + x_2/a_{inf} + x_3.$ 

### <sup>29</sup> S2 How reputation knowledge depends on observing and remember-

<sup>31</sup> Here we derive expressions for the probabilities that a discriminator has an opinion <sup>32</sup> about another agent and that a discriminator has a good opinion about another dis-<sup>33</sup> criminator. We also prove two relations involving these probabilities that are useful for <sup>34</sup> analyzing the replicator dynamics of our model.

We use  $k_i(t)$  to denote the probability that a discriminator has an opinion about an 35 agent of type *i* at time *t*. The sum of these probabilities over all rounds,  $K_i = \sum_{t=1}^{R} k_i(t)$ , 36 depends on the information parameters  $p_0$  and  $p_r$ , the degree of information assortment 37  $a_{inf}$ , and the number *R* of rounds. We use g(t) to denote the probability that a discrimi-38 nator has a good opinion about another discriminator at time t. The sum of these prob-39 abilities over all rounds,  $G = \sum_{t=1}^{R} g(t)$ , depends on the information parameters  $p_0$  and 40  $p_{\rm r}$ , the degree of information assortment  $a_{\rm inf}$ , and the number R of rounds, but also on 41 the observed behaviors of the discriminators, and hence on the degree of interaction as-42 sortment  $a_{int}$  and on the frequencies of the three types of agents,  $x_1$ ,  $x_2$ , and  $x_3$ . We some-43 times write  $g_{x_1,x_3}(t)$  and  $G_{x_1,x_3}$  to emphasize the latter dependence (bearing in mind that 44  $x_2 = 1 - x_1 - x_3$ ). In the following, we write  $x_{ij}$  for the frequency with which an agent 45 of type *i* interacts with an agent of type *j*. For example,  $x_{33} = a_{int}x_3/(x_1 + x_2 + a_{int}x_3)$ . 46

We denote by  $p_{o,i}$  the probability of a focal agent be observed by a discriminator, given he is of type *i*. For example,  $p_{o,3} = x_{33}/x_3 = p_o a_{inf}/(x_1 + x_2 + a_{inf}x_3)$ .

<sup>49</sup> A discriminator has an opinion about another agent at time *t* if he has observed the <sup>50</sup> other agent at time t - 1 and remembers that observation or if he did not observe the <sup>51</sup> other agent but had an opinion about him at time t - 1 and remembers that opinion. <sup>52</sup> This establishes a recursive equation for how  $k_i(t)$  depends on  $k_i(t - 1)$ ,

$$k_i(t) = p_r p_{o,i} + k_i(t-1)p_r(1-p_{o,i}).$$

<sup>54</sup> We can then show inductively that if  $k_i(1) = 0$ ,  $k_i(t)$  for t > 1 is given by

55 
$$k_i(t) = p_r p_{o,i} \frac{1 - p_r^{t-1} (1 - p_{o,i})^{t-1}}{1 - p_r (1 - p_{o,i})},$$

56 which yields

53

57 
$$K_{i} = \sum_{t=1}^{R} k_{i}(t) = \frac{Rp_{r}p_{o,i}}{1 - p_{r}(1 - p_{o,i})} - \frac{p_{r}p_{o,i}(1 - p_{r}^{R}(1 - p_{o,i})^{R})}{(1 - p_{r}(1 - p_{o,i}))^{2}}.$$

Analogously, a discriminator has a good opinion about another discriminator at time t if he has observed the discriminator donating at time t - 1 and remembers that observation, or if he did not observe the other discriminator but had a good opinion about him at time t - 1 and remembers that opinion. A discriminator donates to cooperators of whom he has an opinion, to discriminators of whom he has a good opinion, and with probability  $p_c$  to agents he does not know about. This establishes a recursive equation

for how g(t) depends on  $k_i(t-1)$  and g(t-1), 64

$$g_{x_{1},x_{3}}(t) = p_{r}p_{o,3}\left(k_{1}(t-1)x_{31} + g_{x_{1},x_{3}}(t-1)x_{33} + p_{c}\left(1 - \sum_{i=1}^{3} x_{3i}k_{i}(t-1)\right)\right) + p_{r}(1 - p_{o,3})g_{x_{1},x_{3}}(t-1)$$

66

67

$$= p_{\rm r} p_{{\rm o},3} p_{\rm c} + p_{\rm r} p_{{\rm o},3} k_1 (t-1) x_{31} - p_{\rm r} p_{{\rm o},3} p_{\rm c} \sum_{i=1}^3 x_{3i} k_i (t-1)$$

$$+ p_{\rm r}(p_{{\rm 0},3}x_{33} + 1 - p_{{\rm 0},3})g_{x_1,x_3}(t-1)$$

<sup>69</sup> = 
$$p_r p_{o,3} p_c + p_r p_{o,3} k_1 (t-1) x_{31} - p_r p_{o,3} p_c ((1-x_{33})k_1(t-1) + x_{33}k_3(t-1)))$$

$$+ p_{r}(p_{0,3}x_{33} + 1 - p_{0,3})g_{x_1,x_3}(t-1) \text{ since } p_{0,1} = p_{0,2} \text{ and therefore } k_1 = k_2.$$

Since this recursive equation does not yield a convenient closed-form expression for 72  $G_{x_1,x_3}$ , we determine  $G_{x_1,x_3}$  numerically. 73

Our model reverts to that of ? when there is no assortment and discriminators have 74 perfect information ( $a_{inf} = a_{int} = p_o = p_r = 1$ ). (Nowak & Sigmund also considered a 75 case with limited information, but rather than keeping track of observations and mem-76 ories at each point in time, they assumed that discriminators have a fixed probability 77 of knowing about their peers, so their analysis of a model with limited information is 78 not directly comparable to our model when  $p_0, p_r < 1$ .) ? derived equations for their 79 equivalent of G. Here we extend some of their results to allow for assortment and the 80 mechanism for information gathering described in the main text. The lemmas stated 81 below allow us to simplify the payoff functions for the three types of agents, given in 82 Section S3, and recover statements made by ? for  $a_{inf} = a_{int} = p_o = p_r = 1$ . 83

**Lemma S.1**  $G_{0,1} = p_c K_3$ . 84

*Proof.* It suffices to show that  $g_{0,1}(t) = p_c k_3(t)$  for every *t*. We prove this by induction 85

<sup>86</sup> on *t*. First we consider t = 1, 2,

 $g_{0,1}(1) = 0 = p_c k_3(1)$  and

$$g_{0,1}(2) = p_{\rm r} p_{\rm o} p_{\rm c} = p_{\rm c} k_3(2).$$

<sup>90</sup> Thus, the claim is true for t = 1, 2. Now we assume the claim is true up to t - 1,

$$g_{0,1}(t) = p_{\rm r} p_{{\rm o},3} p_{\rm c} - p_{\rm r} p_{{\rm o},3} p_{\rm c} k_3(t-1) + p_{\rm r} (p_{{\rm o},3} + 1 - p_{{\rm o},3}) g_{0,1}(t-1)$$

$$= p_r p_{o,3} p_c - p_r p_{o,3} p_c k_3(t-1) + p_r p_c k_3(t-1)$$
 by the inductive hypothesis

<sup>93</sup> 
$$= p_{\rm c} (p_{\rm r} p_{{\rm o},3} + p_{\rm r} (1 - p_{{\rm o},3}) k_3 (t - 1))$$

<sup>96</sup> Thus, the claim is proved.

 $= p_{\rm c}k_3(t).$ 

### Lemma S.2

$$G_{x_1,x_3} - G_{0,x_3} = \frac{x_{31}}{p_c(1-x_{33})}(p_cK_3 - G_{0,x_3}).$$

Proof. It suffices to show that  $g_{x_1,x_3}(t) - g_{0,x_3}(t) = \frac{x_{31}}{p_c(1-x_{33})}(p_ck_3(t) - g_{0,x_3}(t))$  for every t. We prove this by induction on t. First we consider t = 1, 2,

$$g_{x_1,x_3}(1) = g_{0,x_3}(1) = k_3(1) = 0$$

$$\Rightarrow g_{x_1,x_3}(1) - g_{0,x_3}(1) = 0 = \frac{x_{31}}{p_{c}(1-x_{33})} (p_{c}k_3(1) - g_{0,x_3}(1)),$$

and 
$$g_{x_1,x_3}(2) = g_{0,x_3}(2) = p_r p_{0,3} p_c$$
,  $k_3(2) = p_r p_{0,3}$ ,

$$\Rightarrow g_{x_1,x_3}(2) - g_{0,x_3}(2) = 0 = \frac{x_{31}}{p_c(1-x_{33})} (p_c k_3(2) - g_{0,x_3}(2)).$$

<sup>104</sup> Thus, the claim is true for t = 1, 2. Now we assume the claim is true up to t - 1,

<sup>105</sup> 
$$g_{x_1,x_3}(t) = p_r p_{0,3} p_c + p_r p_{0,3} k_1(t-1) x_{31} - p_r p_{0,3} p_c ((1-x_{33})k_1(t-1) + x_{33}k_3(t-1)))$$

106 + 
$$p_{r} (p_{o,3}x_{33} + 1 - p_{o,3}) g_{x_{1},x_{3}}(t-1)$$

$$= p_{r}p_{0,3}p_{c} + p_{r}p_{0,3}k_{1}(t-1)x_{31} - p_{r}p_{0,3}p_{c}\left((1-x_{33})k_{1}(t-1) + x_{33}k_{3}(t-1)\right)$$

$$+ p_{\rm r} \left( p_{\rm o,3} x_{33} + 1 - p_{\rm o,3} \right) \left( g_{0,x_3}(t-1) + \frac{x_{31}}{p_{\rm c}(1-x_{33})} \left( p_{\rm c} k_3(t-1) - g_{0,x_3}(t-1) \right) \right)$$

<sup>109</sup> by the inductive hypothesis

$$= p_{\rm r} p_{\rm o,3} p_{\rm c} - p_{\rm r} p_{\rm o,3} p_{\rm c} \left( (1 - x_{33}) k_1 (t - 1) + x_{33} k_3 (t - 1) \right) + p_{\rm r} \left( p_{\rm o,3} x_{33} + 1 - p_{\rm o,3} \right) g_{0,x_3} (t - 1)$$

$$+ \frac{x_{31}}{p_{c}(1-x_{33})} (p_{r}p_{o,3}p_{c}(1-x_{33})k_{1}(t-1) + p_{r}(p_{o,3}x_{33}+1-p_{o,3})p_{c}k_{3}(t-1)$$

<sup>112</sup> 
$$- p_{\rm r} \left( p_{{\rm o},3} x_{33} + 1 - p_{{\rm o},3} \right) g_{0,x_3}(t-1)$$

<sup>113</sup> = 
$$g_{0,x_3}(t) + \frac{x_{31}}{p_c(1-x_{33})}(p_c p_r p_{0,3} + p_c p_r(1-p_{0,3})k_3(t-1) +$$

<sup>114</sup> 
$$- p_{c}p_{r}p_{0,3} + p_{r}p_{0,3}p_{c}((1-x_{33})k_{1}(t-1) + x_{33}k_{3}(t-1))$$

<sup>115</sup> 
$$- p_{\rm r} \left( p_{{\rm o},3} x_{33} + 1 - p_{{\rm o},3} \right) g_{0,x_3}(t-1) \right)$$

$$= g_{0,x_3}(t) + \frac{x_{31}}{p_c(1-x_{33})} \left( p_c k_3(t) - g_{0,x_3}(t) \right).$$

<sup>118</sup> Thus, the claim is proved.

### **119 S3 Derivation of payoffs**

Here we derive expressions for the expected payoffs  $\hat{P}_i$  of agents of type *i*, as well as a condition that must be satisfied at equilibrium.

For each of the three types, an agent's expected payoff depends on his own behavior, the behaviors of the other types, and the frequencies of all three types. The payoffs also depend on how assorted the discriminators are in their interactions. In the following, we write  $x_{ij}$  for the frequency with which an agent of type *i* interacts with an agent of type *j*. For example,  $x_{33} = a_{int}x_3/(x_1 + x_2 + a_{int}x_3)$ . As explained in Section S2,  $K_i$  describes how likely a discriminator is to know about an agent of type *i* and *G* describes how likely a discriminator is to consider another discriminator as good.

<sup>129</sup> For cooperators,

130

135

$$\hat{P}_1 = bRx_{11} + bp_c(R - K_1)x_{13} + bK_1x_{13} - cR,$$

since a cooperator receives a donation from any other cooperator, with probability  $p_c$ from any discriminator who does not have an opinion about him, and from any discriminator who has an opinion about him, and since a cooperator always donates. For defectors,

$$\hat{P}_2 = bRx_{21} + bp_{\rm c}(R - K_2)x_{23},$$

since a defector receives a donation from any cooperator and with probability  $p_c$  from any discriminator who does not have an opinion about him, and since a defector never donates. For discriminators,

$$\hat{P}_{3} = bRx_{31} + bp_{c}(R - K_{3})x_{33} + bGx_{33} - c\left(R - \sum_{i=1}^{3} x_{3i}K_{i}\right)p_{c} - cK_{1}x_{31} - cGx_{33} - s,$$

since a discriminator receives a donation from any cooperator, with probability  $p_c$  from any discriminator who does not have an opinion about him, and from any discriminator who has a good opinion about him, since a discriminator donates with probability  $p_c$  to any unknown agent, to any cooperator he has an opinion about, and to any discriminator he has a good opinion about, and since discriminators pay a cost for their information gathering and storage. We can subtract the same quantity from all payoff functions without affecting the resulting replicator dynamics (?), so for simplicity we subtract  $\hat{P}_2$  <sup>147</sup> from each expected payoff, giving

148  $P_1 = \hat{P}_1 - \hat{P}_2,$ 149  $P_2 = 0,$ 

$$P_3 = \hat{P}_3 - \hat{P}_2.$$

According to the replicator dynamics, a group reaches an equilibrium when either  $x_i = 0$  or  $P_i = \overline{P}$  for each *i*. Here we derive expressions for  $P_1$  and  $P_3$  when  $a_{int} = 1$ . It is always the case that  $K_1 = K_2$ . When  $a_{int} = 1$ ,  $x_{1i} = x_{2i} = x_{3i} = x_i$  for i = 1, 2, 3. In this case,

<sup>156</sup>  $P_1 = bK_1x_3 - cR,$ <sup>157</sup>  $P_2 = 0,$ <sup>158</sup>  $P_3 = bp_cx_3(K_1 - K_3) + (b - c)G_{x_1,x_3}x_3 - c(R - (1 - x_3)K_1 - x_3K_3)p_c - cK_1x_1 - s$ <sup>159</sup>  $= (b - c)G_{x_1,x_3}x_3 - c(R - K_1)p_c - cx_3(K_1 - K_3)p_c - cK_1x_1 - s.$ 

<sup>161</sup> In Section S2, we proved (Lemma S.2) that

<sup>162</sup> 
$$G_{x_1,x_3} - G_{0,x_3} = \frac{x_1}{p_c(1-x_3)}(p_cK - G_{0,x_3}).$$

If  $a_{int} = 1$ , we can use this to rewrite  $P_3 - \bar{P}$ , 163

\_

$$\begin{array}{rcl} & P_{3}-\bar{P}=(1-x_{3})P_{3}-x_{1}P_{1}\\ & =(1-x_{3})bp_{c}x_{3}(K_{1}-K_{3})+(1-x_{3})x_{3}(b-c)G_{x_{1},x_{3}}-(1-x_{3})c(R-K_{1})p_{c}\\ & -(1-x_{3})x_{3}c(K_{1}-K_{3})p_{c}-x_{1}(1-x_{3})cK_{1}-s(1-x_{3})-x_{1}x_{3}bK_{1}+x_{1}cR\\ & =(1-x_{3})bp_{c}x_{3}(K_{1}-K_{3})+(1-x_{3})x_{3}(b-c)\left(G_{0,x_{3}}+\frac{x_{1}}{p_{c}(1-x_{3})}(p_{c}K_{3}-G_{0,x_{3}})\right)\\ & -p_{c}(1-x_{3})c(R-K_{1})+x_{1}c(R-K_{1})-x_{1}x_{3}(b-c)K_{1}-p_{c}(1-x_{3})x_{3}c(K_{1}-K_{3})-s(1-x_{3})\\ & =x_{3}(b-c)\frac{p_{c}(1-x_{3})-x_{1}}{p_{c}}G_{0,x_{3}}+x_{1}x_{3}(b-c)K_{3}-p_{c}(1-x_{3})c(R-K_{1})+x_{1}c(R-K_{1})\\ & -x_{1}x_{3}(b-c)K_{1}+p_{c}(1-x_{3})x_{3}(b-c)(K_{1}-K_{3})-s(1-x_{3})\\ & =\frac{p_{c}(1-x_{3})-x_{1}}{p_{c}}\left(x_{3}(b-c)x_{3}G_{0,x_{3}}+x_{3}(b-c)p_{c}(K_{1}-K_{3})-cp_{c}(R-K_{1})\right)-s(1-x_{3})\\ \end{array}$$

$$= \frac{p_{\rm c}(1-x_3)-x_1}{p_{\rm c}} \left( (b-c)x_3(G_{0,x_3}+p_{\rm c}(K_1-K_3))-cp_{\rm c}(R-K_1) \right) - s(1-x_3).$$

If s = 0, any equilibrium with discriminators at non-zero frequency must satisfy either 174  $p_{\rm c}(1-x_3) - x_1 = 0$  or 175

<sup>176</sup> 
$$(b-c)x_3(G_{0,x_3}+p_c(K_1-K_3))-cp_c(R-K_1)=0.$$

If s > 0, any equilibrium with discriminators at non-zero frequency must satisfy 177

<sup>178</sup> 
$$(b-c)x_3(G_{0,x_3}+p_c(K_1-K_3))=c(R-K_1)p_c+\frac{sp_c(1-x_3)}{p_c(1-x_3)-x_1}.$$

These conditions describe lines and curves in the simplex whose intersections with the 179 simplex borders or with a line on which  $P_1 = P_2$  determine the locations of the replicator 180 dynamics' equilibria. 181

#### Changing the probability of donating to an unknown agent **S**4 182

For most of our analyses in the main text, the probability  $p_c$  that a discriminator donates 183 to an unknown agent is set to 0.5. Here we investigate the robustness of our results to 184

<sup>185</sup> other choices of  $p_c$ .

Our main results are that, when discriminators have sufficient information about 186 their peers and when interactions are negatively assorted or observations are positively 187 assorted, a stable cooperator-discriminator equilibrium can be reached. Additionally, 188 increasing the amount of information available to discriminators can allow defectors to 189 invade such a stable cooperator-discriminator equilibrium. Assuming s = 0, if the in-190 teraction assortment  $a_{int}$ , information assortment  $a_{inf}$ , probability  $p_0$  of observing, and 191 probability  $p_r$  of remembering allow for a stable mixture of cooperators and discrimina-192 tors for  $p_c = 0.5$ , this equilibrium will exist and will be stable for all values of  $p_c < 1$ . 193 This means that the boundaries of the dark blue regions in Figures 1 and 2 are the same 194 for any value of  $p_c < 1$ . This can be seen in Figures S4-S7. Similarly, if a stable interior 195 equilibrium exists for  $p_c = 0.5$ , it will exist for all values of  $0.5 < p_c < 1$  (Figures S4 and 196 S6) and for values of  $p_c$  that can be as low as 0.1 (Figures S5 and S7). 197

The extreme case when  $p_c = 1$  does change the dynamics slightly. For  $p_c = 1$ , 198 discriminators always donate to unknown agents. In the absence of defectors, a dis-199 criminator will always cooperate, so the edge of the simplex between discriminators 200 and cooperators becomes neutral. In other words, every point on the edge becomes an 201 equilibrium (as can be seen by the line of points along the left edge of the simplexes 202 in the right-most columns of Figures S4 and S6). However, the directions of trajecto-203 ries to or from the interior of the simplex are unchanged. If there was either a stable 204 cooperator-discriminator equilibrium or a stable interior equilibrium for  $p_c$  just below 205 1, for  $p_c = 1$ , trajectories that start at the top of the simplex will move toward the 206 cooperator-discriminator edge, while trajectories that start at the bottom of the simplex 207 will move toward the pure defector equilibrium (Figures S4 and S6). While there is no 208 longer a *unique* stable cooperative equilibrium, it can still be said that discriminators 209

can keep defectors at bay. Similarly, in the extreme case when  $p_c = 0$ , the edge of the simplex between discriminators and defectors becomes neutral. Again, the directions of trajectories to or from this edge remain unchanged.

The replicator dynamics can be changed by varying  $p_c$ . If there is a stable interior 213 equilibrium when  $p_c = 0.5$ , this can be destabilized when  $p_c$  is low enough (Figures S5) 214 and S7). In this case, discriminators cooperate so rarely with strangers that their help 215 is no longer sufficient to maintain cooperators in the group. This means that parts of 216 the light-blue regions in Figures 1 and 2 can turn red when  $p_c$  increases. Additionally, 217 the neutral centers indicated by the white regions in Figures 1 and 2 are affected by  $p_c$ . 218 When  $a_{int} < 1$ , the center is stabilized as soon as  $p_c > 0.5$  and destabilized as soon as 219  $p_{\rm c}$  < 0.5 (Figures S4 and S5). Conversely, when  $a_{\rm int}$  > 1, the center is destabilized as 220 soon as  $p_c > 0.5$  and stabilized as soon as  $p_c < 0.5$  (Figures S4 and S5). This means that 221 parts of the white region in Figure 1 can turn either light-blue or red. 222

We can, in fact, show mathematically that if a cooperator-discriminator equilibrium exists for  $p_c = 0.5$ , it will exist for all values  $p_c < 1$ . For this, we consider the expected payoffs in a group consisting only of defectors and discriminators, i.e., at a point given by the frequency combination  $p_2 = (0, 1 - x_3, x_3)$ , when the cost of information is zero, s = 0,

228

$$P_2 = b p_c (R - K_2) x_{23},$$

$$\hat{P}_3 = bp_c(R - K_3)x_{33} + (b - c)G_{0,x_3}x_{33} - cp_c(R - K_2x_{32} - K_3x_{33}).$$

If this point is an equilibrium,  $\hat{P}_2 = \hat{P}_3$ , and thus

$$bp_{c}(R-K_{2})x_{23} = bp_{c}(R-K_{3})x_{33} + (b-c)G_{0,x_{3}}x_{33} - cp_{c}(R-K_{2}x_{32} - K_{3}x_{33}).$$
 (S1)

It is clear from the definition of *G* that  $G_{0,x_3}$  is proportional to  $p_c$ . This means that, in the absence of cooperators, the total payoffs to both defectors and discriminators are

proportional to  $p_{\rm c}$ . This makes sense, since discriminators cooperate with defectors only 236 when the latter are unknown to them, an occurrence dictated by  $p_c$ , and the probabil-237 ity of a discriminator being considered good by other discriminators is dictated by his 238 initial random acts of cooperation, also dictated by  $p_c$ . Consequently, if  $\hat{P}_2 = \hat{P}_3$  for any 239 particular value of  $p_c$ , it follows that  $\hat{P}_2 = \hat{P}_3$  for all values of  $p_c$ . Therefore, if  $p_2$  is an 240 equilibrium for any value of  $p_c$ , it will be an equilibrium for all values of  $p_c$ . 241

Next, we consider the point given by the frequency combination  $p_1 = (1 - x_3, 0, x_3)$ . 242 We now show that, if  $p_2 = (0, 1 - x_3, x_3)$  is an equilibrium,  $p_1$  will also be an equilibrium. 243 It is always true that  $K_1 = K_2$ . It is also true that  $x_{23}$  at  $p_2$  equals  $x_{13}$  at  $p_1$  and that  $x_{32}$  at 244  $p_2$  equals  $x_{31}$  at  $p_1$ . Hence, if S1 holds at  $p_2$ , 245

$$bp_{c}(R-K_{1})x_{13} = bp_{c}(R-K_{3})x_{33} + (b-c)G_{0,x_{3}}x_{33} - cp_{c}(R-K_{1}x_{31} - K_{3}x_{33})$$
(S2)

will hold at  $p_1$ . Therefore, 248

- $bp_{c}(R-K_{1})x_{13} = bp_{c}Rx_{33} + (b-c)(G_{0,x_{2}}x_{33} p_{c}K_{3})x_{33} cp_{c}(R-K_{1}x_{31})$ 249  $= bp_{c}Rx_{33} + (b-c)p_{c}(G_{0,x_{3}}x_{33} - G_{x_{1},x_{3}})x_{33} - cp_{c}(R - K_{1}x_{31})$ 250
- 251

255

using Lemma S.2

$$\Rightarrow b(R - K_1)x_{13} = bRx_{33} + (b - c)(G_{0,x_3}x_{33} - G_{x_1,x_3})x_{33} - c(R - K_1x_{31}) \Rightarrow bR - bRx_{11} - bK_1x_{13} = bR - bRx_{31} + (b - c)(G_{0,x_3}x_{33} - G_{x_1,x_3})x_{33} - cR + cK_1x_{31} \Rightarrow bRx_{11} + bK_1x_{13} - cR = bRx_{31} - cK_1x_{31} + (b - c)(G_{x_1,x_3}x_{33} - G_{0,x_3})x_{33}.$$
 (S3)

Combining Equations S2 and S3, we find that  $\hat{P}_1 = \hat{P}_3$  at  $p_1$ , so that  $p_1$  is also an equi-256 librium. Thus, if  $p_1$  is an equilibrium at any value of  $p_c$ , it will be an equilibrium for all 257 values of  $p_{\rm c}$ . 258

### <sup>259</sup> S5 Bifurcation analysis

Here we identify and explain the various bifurcations occurring in the replicator dynam ics of our model.

We assess the stability of each equilibrium discussed here by numerically calculating 262 the eigenvalues of the Jacobian of the replicator dynamics there. The transition from B to 263 C in Figure ?? involves two transcritical bifurcations. First, an equilibrium to the left of 264 the simplex moves to the interior, exchanging stability in the direction toward the inte-265 rior of the simplex with the cooperator-discriminator equilibrium. Thus, the cooperator-266 discriminator equilibrium changes from a stable node to a saddle and a stable interior 267 equilibrium appears. Simultaneously, an equilibrium to the right of the simplex moves 268 to the interior, exchanging stability in the direction toward the interior of the simplex 269 with the defector-discriminator equilibrium. Thus, the defector-discriminator equilib-270 rium changes from an unstable node to a saddle and an unstable interior equilibrium 271 appears. 272

The transition from C to D in Figure **??** involves a saddle-node bifurcation, as the three interior equilibria collide: the equilibria on the left and right annihilate each other and the middle equilibria changes from a saddle to a neutral center.

The transition from D to E in Figure ?? involves two transcritical bifurcations. First, 276 an equilibrium to the left of the simplex moves to the interior, exchanging stability in 277 the direction toward the interior of the simplex with the cooperator-discriminator equi-278 librium. Thus, the cooperator-discriminator equilibrium changes from a saddle to a 279 stable node and a saddle appears in the interior. Simultaneously, an equilibrium to 280 the right of the simplex moves to the interior, exchanging stability in the direction to-281 ward the interior of the simplex with the defector-discriminator equilibrium. Thus, the 282 defector-discriminator equilibrium changes from a saddle to an unstable node and a 283

<sup>284</sup> saddle appears in the interior.

The transition from D to F in Figure **??** involves a saddle-node bifurcation that results in the appearance of a stable node and an unstable node on the cooperator-defector edge. The neutral center moves from the interior of the simplex to the exterior and becomes a saddle.

The transition from B to C in Figure **??** involves a saddle-node bifurcation that results in the appearance of a stable node and an unstable node on the left and right edges of the simplex, respectively. Simultaneously, a saddle that was above the simplex on its exterior moves to the interior.

The transition from C to D in Figure ?? involves two transcritical bifurcations. First, 293 an equilibrium to the left of the simplex moves to the interior, exchanging stability in 294 the direction toward the interior of the simplex with the cooperator-discriminator equi-295 librium. Thus, the cooperator-discriminator equilibrium changes from a stable node to 296 a saddle and a stable interior equilibrium appears. Simultaneously, an equilibrium to 297 the right of the simplex moves to the interior, exchanging stability in the direction to-298 ward the interior of the simplex with the defector-discriminator equilibrium. Thus, the 299 defector-discriminator equilibrium changes from an unstable node to a saddle and an 300 unstable interior equilibrium appears. 30

The transition from B to C in Figure **??** involves a transcritical bifurcation. An equilibrium to the left of the simplex moves to the interior, exchanging stability in the direction toward the interior of the simplex with the cooperator-discriminator equilibrium. Thus, the cooperator-discriminator equilibrium changes from a stable node to a saddle and a stable interior equilibrium appears.

The transition from C to D in Figure **??** involves a saddle-node bifurcation. The stable node and the saddle in the interior of the simplex collide and annihilate each other.

14





Figure S1: No amount of information can stabilize cooperation if there is neither information assortment nor interaction assortment. In (A), we show how the replicator dynamics depend on the probabilities  $p_0$  of observing and  $p_r$  of remembering. The parameter space is colored according to the most cooperative outcome of the replicator dynamics that occurs for a given combination of these parameters. Caption continued below.

Figure S1: A group made up entirely of defectors is always at a stable equilibrium. In the red region, it is the only stable equilibrium. In the white region, a neutral interior equilibrium exists, but a group made up entirely of defectors is still the only stable equilibrium. The horizontal axis extends until  $p_0 = a_{inf}$ , beyond which  $p_0$  is not meaningful (see the Supporting Information, Section S1). In the phase portraits (B)-(C), trajectories show how the frequencies of cooperators, defectors, and discriminators change over time. The lower left corner of the simplex represents a group made up entirely of cooperators, the lower right corner a group made up entirely of defectors, and the upper corner a group made up entirely of discriminators. The colors in the simplices indicate the basins of attraction of the (possibly multiple) stable equilibria. Unstable equilibria are indicated with white circles, neutral centers with gray circles, saddles with half white and half black circles, and stable equilibria with black circles. In (B), all trajectories that start within the simplex eventually move toward the equilibrium made up entirely of discriminators. In (C), trajectories that start in the white region cycle around the neutral center. Parameters: in B,  $p_r = 0.05$ ; in C,  $p_r = 0.95$ ; in all panels,  $p_o = 0.85$ ,  $a_{int} = a_{inf} = 1$ , R = 10, b = 10, c = 1,  $p_c = 0.5$ , and s = 0.



Figure S2: As the number *R* of rounds increases, less assortment is needed to stabilize the cooperator-discriminator equilibrium, and in the limit of infinitely many rounds, any assortment suffices to stabilize the equilibrium. The horizontal axis shows the number *R* of rounds for which the game is played (on a logarithmic scale) and the vertical axis shows the degree of information assortment  $a_{inf}$  or interaction assortment  $a_{int}$  required to stabilize the cooperator-discriminator equilibrium, while the other assortment parameter is fixed at 1. Parameters:  $p_r = 0.95$ ,  $p_o = 0.85$ , b = 10, c = 1,  $p_c = 0.5$ , and s = 0.



Figure S3: The more rounds *R* a group plays and the greater the benefit *b* of cooperation, the less information is required to stabilize cooperation. Each line separates the parameter space of the probabilities  $p_0$  of observing and  $p_r$  of remembering into two regions: above the line, information suffices to stabilize either a cooperator-discriminator equilibrium or an interior equilibrium, whereas below the line, information is insufficient to do so. (This transition also occurs at the boundary between the red and dark-blue regions in Figure 2A.) Parameters:  $a_{int} = a_{inf} = 0.93$ , c = 1,  $p_c = 0.5$ , and s = 0.



Figure S4: Caption below.

Figure S4: Increasing the probability  $p_c$  of cooperating with unknown agents does not change the existence or stability of cooperator-discriminator equilibria. In the left column, the phase portraits are as in Figure 1. The one difference is that, whereas in Figure 1 we showed a neutral interior equilibrium for the single parameter combination  $a_{int} = a_{inf} = 1$ , here we show two other parameter combinations that give rise to a neutral interior equilibrium, the first with both assortment parameters less than 1 and the second with both assortment parameters greater than 1. Moving from top to bottom, from one panel to the next either one or both of the assortment parameters,  $a_{int}$  and  $a_{inf}$ , increase. Moving from left to right,  $p_c$  increases until it equals 1. In each phase portrait, trajectories show how the frequencies of cooperators, defectors, and discriminators change over time. The lower left corner of the simplex represents a group made up entirely of cooperators, the lower right corner a group made up entirely of defectors, and the upper corner a group made up entirely of discriminators. The colors in the simplices indicate the basins of attraction of the stable equilibria or a region in which trajectories cycle around a neutral center. Unstable equilibria are indicated with white circles, stable equilibria with black circles, saddles with half white and half black circles, and neutral centers with gray circles. If there is a stable cooperator-discriminator equilibrium for  $p_{\rm c} = 0.5$ , this will persist for all values  $0.5 < p_{\rm c} < 1$ , as seen in (A)-(D) and (Q)-(T). If there is a stable interior equilibrium for  $p_c = 0.5$ , this will persist for all values  $0.5 < p_c < 1$ , as seen in (E)-(H). If there is a neutral equilibrium for  $p_c = 0.5$ , this can be either stabilized or destabilized by increasing  $p_c$  when  $a_{int}$  is greater than or less than 1, respectively, as seen in (I)-(L) and (M)-(P). If there is a stable cooperator-defector equilibrium for  $p_c = 0.5$ , this will persist for all values of  $0.5 \le p_c \le 1$ , as seen in (U)-(X). Caption continued below.

Figure S4: Our model's replicator dynamics do change at the extreme value of  $p_c = 1$ . All points on the cooperator-discriminator edge become neutral equilibria along that edge of the simplex. Additionally, a stable interior equilibrium may collide with that edge of the simplex and disappear, as seen in the transition from (K) to (L). The directions of trajectories to or from the interior of the simplex remain unchanged: the upper part of the edge attracts trajectories from the interior, while trajectories move away from points on the lower part of the edge. This is indicated with points that are half gray and half white or black, depending on whether trajectories from the interior approach or move away from the edge there, respectively. Parameters: in A-D,  $a_{int} = 0.93$ ,  $a_{inf} = 0.93$ ; in E-H,  $a_{int} = 0.98$ ,  $a_{inf} = 0.98$ ; in I-L,  $a_{int} = 0.995$ ,  $a_{inf} = 0.9$ ; in M-P,  $a_{int} = 1.005$ ,  $a_{inf} = 1.005$ ; in Q-T,  $a_{int} = 1.005$ ,  $a_{inf} = 1.17$ ; in U-X,  $a_{int} = 1.24$ ,  $a_{inf} = 1.17$ ; in the left-most column,  $p_c = 0.5$ ; in the second column,  $p_c = 0.9$ ; in the third column,  $p_c = 0.97$ ; in the right-most column,  $p_c = 1$ ; in all panels,  $p_0 = 0.85$ ,  $p_r = 0.95$ , R = 10, b = 10, c = 1, and s = 0.



Figure S5: Caption below.

Figure S5: Decreasing the probability  $p_c$  of cooperating with unknown agents does not change the existence or stability of a cooperator-discriminator equilibria. In the left column, the phase portraits are as in Figure 1. The one difference is that, whereas in Figure 1 we showed a neutral interior equilibrium for the single parameter combination  $a_{int} = a_{inf} = 1$ , here we show two other parameter combinations that give rise to a neutral interior equilibrium, the first with both assortment parameters less than 1 and the second with both assortment parameters greater than 1. Moving from top to bottom, from one panel to the next either one or both of the assortment parameters,  $a_{int}$  and  $a_{inf}$ , increase. Moving from left to right,  $p_c$  decreases until it equals 0. In each phase portrait, trajectories show how the frequencies of cooperators, defectors, and discriminators change over time. The lower left corner of the simplex represents a group made up entirely of cooperators, the lower right corner a group made up entirely of defectors, and the upper corner a group made up entirely of discriminators. The colors in the simplices indicate the basins of attraction of the stable equilibria or a region in which trajectories cycle around a neutral center. Unstable equilibria are indicated with white circles, stable equilibria with black circles, saddles with half white and half black circles, and neutral centers with gray circles. If there is a stable cooperator-discriminator equilibrium for  $p_{\rm c}=0.5$ , this will persist for all values of  $0 \le p_{\rm c} \le 0.5$ , as seen in (A)-(D) and (Q)-(T). If there is a stable interior equilibrium for  $p_c = 0.5$ , this will persist until very small values of  $p_c$ , at which the interior equilibrium is destabilized and all trajectories flow toward the pure defector equilibrium, as seen in (E)-(H). If there is a neutral equilibrium for  $p_c = 0.5$ , this can become either destabilized or stabilized when  $a_{int}$  is greater than or less than 1, respectively, as seen in (I)-(L) and (M)-(P). If there is a stable cooperatordefector equilibrium for  $p_c = 0.5$ , this will persist for all values of  $0 \le p_c \le 0.5$ , as seen in (U)-(X). Caption continued below.

Figure S5: Our model's replicator dynamics do change at the extreme value of  $p_c = 0$ . All points on the defector-discriminator edge become neutral equilibria along that edge of the simplex. The direction of trajectories to or from the interior of the simplex remain unchanged: the lower part of the edge attracts trajectories from the interior, while trajectories move away from points on the upper part of the edge. This is indicated with points that are half gray and half white or black, depending on whether trajectories from the interior approach or move away from the edge there, respectively. Parameters: in A-D,  $a_{int} = 0.93$ ,  $a_{inf} = 0.93$ ; in E-H,  $a_{int} = 0.98$ ,  $a_{inf} = 0.98$ ; in I-L,  $a_{int} = 0.995$ ,  $a_{inf} = 0.9$ ; in M-P,  $a_{int} = 1.005$ ,  $a_{inf} = 1.005$ ; in Q-T,  $a_{int} = 1.005$ ,  $a_{inf} = 1.17$ ; in U-X,  $a_{int} = 1.24$ ,  $a_{inf} = 1.17$ ; in the left-most column,  $p_c = 0.5$ ; in the second column,  $p_c = 0.1$ ; in the third column,  $p_c = 0.03$ ; in the right-most column,  $p_c = 0$ ; in all panels,  $p_0 = 0.85$ ,  $p_r = 0.95$ , R = 10, b = 10, c = 1, and s = 0.



Figure S6: Caption below.

Figure S6: Increasing the probability  $p_c$  of cooperating with unknown agents does not change the existence or stability of a cooperator-discriminator equilibrium. In the left column, the phase portraits are as in Figure 2. Moving from top to bottom, the probability  $p_r$  of remembering increases. Moving from left to right,  $p_c$  increases until it equals 1. In each phase portrait, trajectories show how the frequencies of cooperators, defectors, and discriminators change over time. The lower left corner of the simplex represents a group made up entirely of cooperators, the lower right corner a group made up entirely of defectors, and the upper corner a group made up entirely of discriminators. The colors in the simplices indicate the basins of attraction of the stable equilibria or a region in which trajectories cycle around a neutral center. Unstable equilibria are indicated with white circles, stable equilibria with black circles, and saddles with half white and half black circles. If there are no mixed equilibria for  $p_c = 0.5$ , there will be no mixed equilibria for any value  $0.5 \le p_c \le 1$ , as seen in (A)-(D). If there is a stable cooperatordiscriminator equilibrium for  $p_{\rm c}=$  0.5, this will persist for all values 0.5 <  $p_{\rm c}$  < 1, as seen in (E)-(H). If there is a stable interior equilibrium for  $p_c = 0.5$ , this will persist for all values  $0.5 < p_c < 1$ , as seen in (I)-(L). Our model's replicator dynamics do change at the extreme value of  $p_c = 1$ . All points on the cooperator-discriminator edge become neutral equilibria along that edge of the simplex. Additionally, a stable interior equilibrium may collide with that edge of the simplex and disappear, as seen in the transition from (K) to (L). The direction of trajectories to or from the interior of the simplex remain unchanged: the upper part of the edge attracts trajectories from the interior, while trajectories move away from points on the lower part of the edge. This is indicated with points that are half gray and half white or black, depending on whether trajectories from the interior approach or move away from the edge there, respectively. Caption continued below.

Figure S6: Parameters: in A-D,  $p_r = 0.25$ ,  $p_o = 0.3$ ; in E-H,  $p_r = 0.6$ ,  $p_o = 0.3$ ; in I-L,  $p_r = 1$ ,  $p_o = 0.3$ ; in the left-most column,  $p_c = 0.5$ ; in the second column,  $p_c = 0.6$ ; in the third column,  $p_c = 0.9$ ; in the right-most column,  $p_c = 1$ ; in all panels,  $a_{int} = a_{inf} = 0.93$ , R = 10, b = 10, c = 1,  $p_c = 0.5$ , and s = 0.



Figure S7: Caption below.

Figure S7: Decreasing the probability  $p_c$  of cooperating with unknown agents does not change the existence or stability of a cooperator-discriminator equilibria. In the left column, the phase portraits are as in Figure 2. Moving from top to bottom, the probability  $p_{\rm r}$  of remembering increases. Moving from left to right,  $p_{\rm c}$  decreases until it equals 0. In each phase portrait, trajectories show how the frequencies of cooperators, defectors, and discriminators change over time. The lower left corner of the simplex represents a group made up entirely of cooperators, the lower right corner represents a group made up entirely of defectors, and the upper corner represents a group made up entirely of discriminators. The colors in the simplices indicate the basins of attraction of the stable equilibria or a region in which trajectories cycle around a neutral center. Unstable equilibria are indicated with white circles, stable equilibria with black circles, and saddles with half white and half black circles. If there are no mixed equilibria for  $p_c = 0.5$ , then there will be no mixed equilibria for any value  $0 \le p_c \le 0.5$ , as seen in (A)-(D). If there is a stable cooperator-discriminator equilibrium for  $p_c = 0.5$ , this will persist for all values  $0 \le p_c \le 0.5$ , as seen in (E)-(H). If there is a stable interior equilibrium for  $p_c = 0.5$ , this will persist until a value of about  $p_c = 0.4$ , at which the interior equilibrium is destabilized and all trajectories flow toward the pure defector equilibrium, as seen in (I)-(L). Our model's replicator dynamics do change at the extreme value of  $p_c = 0$ . All points on the defector-discriminator edge become neutral equilibria along that edge of the simplex. The direction of trajectories to or from the interior of the simplex remain unchanged: the lower part of the edge attracts trajectories from the interior, while trajectories move away from points on the upper part of the edge. This is indicated with points that are half gray and half white or black, depending on whether trajectories from the interior approach or move away from the edge there, respectively. Caption continued below.

Figure S7: Parameters: in A-D,  $p_r = 0.25$ ,  $p_o = 0.3$ ; in E-H,  $p_r = 0.6$ ,  $p_o = 0.3$ ; in I-L,  $p_r = 1$ ,  $p_o = 0.3$ ; in the left-most column,  $p_c = 0.5$ ; in the second column,  $p_c = 0.4$ ; in the third column,  $p_c = 0.1$ ; in the right-most column,  $p_c = 0$ ; in all panels,  $a_{int} = a_{inf} = 0.93$ , R = 10, b = 10, c = 1,  $p_c = 0.5$ , and s = 0.



Figure S8: Our results are qualitatively similar when the benefit *b* of receiving a donation is reduced. In the main text, we use b = 10. In the top row of this figure, we use b = 5, and in the bottom row, we use b = 2. (A) and (C) are identical to the main panel of Figure 1 in the main text, except for the change in *b* and slightly lower values of  $p_0$  and  $p_r$ . In these panels, we show how the replicator dynamics depend on the degrees of information assortment  $a_{inf}$  and interaction assortment  $a_{int}$ . The axes are scaled logarithmically. The dashed line shows where  $a_{inf} = a_{int}$ . Regardless of the value of *b*, we find that assortment, either in information or in interaction, is necessary, but not sufficient, to stabilize cooperation. Caption continued below.

Figure S8: (B) and (D) are identical to the main panel of Figure 2 in the main text, except for the change in *b*. In these panels, we thus show how our model's replicator dynamics depend on the probabilities  $p_0$  of observing and  $p_r$  of remembering. The horizontal axis extends until  $p_0 = a_{inf}$ , beyond which  $p_0$  is not meaningful (see the Supporting Information, Section S1). Regardless of the value of *b*, even limited information can stabilize cooperation and increasing the amount of information can jeopardize cooperation. In each panel, the parameter space is colored according to the most cooperative outcome of the replicator dynamics that occurs for a given combination of these parameters. A group made up entirely of defectors is always a stable equilibrium. In a red region, it is the only stable equilibrium. In a white region, it is the only stable equilibrium, although a neutral interior equilibrium exists. In a dark-blue region, there is a stable cooperatordiscriminator equilibrium. In a light-blue region, there is a stable equilibrium at which with all three types are present. In a purple region, there is a stable cooperator-defector equilibrium. In (C) and (D), a narrow light-blue region exists between the dark-blue and white regions, which is too small to see at the shown scale. In (C), a stable cooperatordefector equilibrium, indicated by the purple region in (A), appears beyond  $a_{int} = 3$ . Parameters: in A and B, b = 5; in C and D, b = 2, in A and C,  $p_r = 0.8$ ,  $p_o = 0.8$ ; in B and D,  $a_{int} = 0.93$ ,  $a_{inf} = 0.93$ ; in all panels,  $a_{int} = a_{inf} = 0.93$ , R = 10, c = 1,  $p_c = 0.5$ , and s = 0.