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Indirect Reciprocity With Negative Assortment and Limited Information Can Promote Cooperation

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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 broadens the set of circumstances in which it is known that cooperation can be maintained and is one of only a few studies to date that show how negative interaction assortment can promote cooperation.

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Keywords

evolution; game theory; knowledge; replicator dynamics; reputation

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, including ostracism (Tavoni et al., 2012), punishment (Nowak, 2006), and reciprocity (Axelrod & Hamilton, 1981; Killingback & Doebeli, 2002; Panchanathan & Boyd, 2003; Nowak, 2006; Ohtsuki & Iwasa, 2006; Pacheco et al., 2006), 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 engage in repeated interactions (Axelrod & Hamilton, 1981; Killingback & 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., Nowak & Sigmund, 1998a,b; Panchanathan & Boyd, 2003; Brandt & Sigmund, 2004, 2006; Ohtsuki & Iwasa, 2006; Pacheco et al., 2006; Uchida, 2010; Uchida & Sigmund, 2010; Nakamura & Masuda, 2011). (For discussions of direct reciprocity, see e.g., Killingback & 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 & Taborsky, 2005) or away from parts of the

environment that have been depleted by defectors (Pepper & 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., Axelrod & Hamilton, 1981; Pepper & Smuts, 2002; Panchanathan & Boyd, 2004; Doebeli & Hauert, 2005; Fletcher & Doebeli, 2006; Ackermann et al., 2008; Rankin & Taborsky, 2009; Ghang & Nowak, 2015; Roberts, 2015; for an exception see Hauert & Doebeli, 2004), while negative interaction assortment tends to inhibit cooperation (Fletcher & Doebeli, 2006; West & Gardner, 2010; Smead & Forber, 2013; Forber & Smead, 2014).

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. Kreps et al., 1982; Nowak & Sigmund, 1998a,b; Panchanathan & Boyd, 2003; Brandt & Sigmund, 2006; Nakamura & Masuda, 2011). 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. Nowak & Sigmund, 1998a,b; Panchanathan & Boyd, 2003; Nakamura & Masuda, 2011). 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 & 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 (Nelson, 1970; Waddington, 1985; Laughlin et al., 1998; Laughlin, 2001; MacIver et al., 2010).

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 & 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.

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.

Interaction dynamics

Following Nowak & 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 $x_1, x_2, x_3 \geq 0$ 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 $x_1/(x_1 + x_2 + a_{\text{int}}x_3)$, with a defector with probability $x_2/(x_1 + x_2 + a_{\text{int}}x_3)$, or with another discriminator with probability $a_{\text{int}}x_3/(x_1 + x_2 + a_{\text{int}}x_3)$. Interaction probabilities for the other two types are defined analogously. When $a_{\text{int}} = 1$, 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 $a_{\text{int}} > 1$, the group is positively assorted with regard to interactions, with agents being more likely to interact with agents of the same type, whereas

when $a_{\text{int}} < 1$, the group is negatively assorted with regard to interactions, with agents being more likely to interact with agents of different types.

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 $x_1/(x_1 + x_2 + a_{\text{inf}}x_3)$, a defector with probability $x_2/(x_1 + x_2 + a_{\text{inf}}x_3)$, and a discriminator with probability $a_{\text{inf}}x_3/(x_1 + x_2 + a_{\text{inf}}x_3)$. In total, a discriminator observes a fraction p_o of all agents in the group. As fractions of the group, $p_o x_1/(x_1 + x_2 + a_{\text{inf}}x_3)$ are cooperators that are observed by a focal discriminator, $p_o x_2/(x_1 + x_2 + a_{\text{inf}}x_3)$ are observed defectors, $p_o a_{\text{inf}}x_3/(x_1 + x_2 + a_{\text{inf}}x_3)$ are observed discriminators, and $1 - p_o$ 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 ($a_{\text{inf}} \gg 1$), 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 ($a_{\text{inf}} \ll 1$), he can only observe a small fraction of the group. To ensure that discriminators can observe their peers with probability p_o for all group compositions, i.e., for all values of x_1 , x_2 , and x_3 , we therefore require $p_o = \min\{a_{\text{inf}}, 1/a_{\text{inf}}\}$. Details on deriving these bounds on p_o 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 $\min\{a_{\text{int}}, 1/a_{\text{int}}\}$, 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 & 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 derive 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 & 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 & 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 the section entitled Robustness and in the Supporting Information, Section S4 and Figures S4–S7.

In previous models of indirect reciprocity (e.g., Panchanathan & Boyd, 2003; Brandt & Sigmund, 2004, 2006), 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 & Boyd, 2003), it does not always do so (Brandt & 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 $s \geq 0$ is deducted, once at the end of the R rounds of interactions, from the payoff a discriminator has accrued from those interactions.

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.

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 $P_i = \bar{P}$.

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 cooperator-discriminator 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.

Assortment can stabilize cooperation

If there is no assortment ($a_{\text{inf}} = a_{\text{int}} = 1$), 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 (Figure 1D). However, if there is a big enough perturbation, the group can be moved into a regime where defection takes over (Figure 1D) (Nowak & Sigmund, 1998b). In the Supporting Information, Figure S1, we show that the neutral interior equilibrium is the only possible mixed equilibrium when $a_{\text{inf}} = a_{\text{int}} = 1$, 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, Figure S1).

With sufficient positive interaction assortment (i.e., far enough to the right to be in the purple region of Figure 1A), a stable and an unstable cooperator-defector equilibrium appear together (as can be seen in the transition from Figure 1D to Figure 1F). 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 cooperator-discriminator 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 Figure 1D to Figure 1C). 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 cooperator-discriminator equilibrium is high enough that the discriminators can prevent defectors from invading and the equilibrium is stabilized (as seen in the transition from Figure 1C to Figure 1B).

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 from Figure 1D to Figure 1E). 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 Figure 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, Figure 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 the section entitled Robustness.

Even limited information can stabilize cooperation

For discriminators to operate and to be able to stabilize cooperation, the probabilities p_o of observing and p_r of remembering both need to exceed 0 (Figure 2A). Increasing p_o and p_r from 0 decreases the benefits defectors receive from discriminators to whom they are unknown. When p_o and p_r are sufficiently high, a stable cooperator-discriminator equilibrium appears (as seen in the transition from Figure 2B to Figure 2C). 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_o 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 Figure 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).

Increasing the probabilities of observing or remembering can help defectors invade

Surprisingly, if the probabilities p_o of observing and p_r of remembering are low but sufficient to stabilize the cooperator-discriminator equilibrium, increasing them further can allow defectors to invade and coexist with cooperators and discriminators at a stable interior equilibrium (as seen in the transition from Figure 2C to Figure 2D and in Figure 3A and C). From there, a stable cooperator-discriminator equilibrium can be recovered by increasing p_o further until the stable interior equilibrium disappears, as seen in Figure 2A and Figure 3A. As the interior equilibrium appears, the probability of any type of agent receiving a donation decreases because of the presence of defectors (Figure 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_o 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 (Figure 3A and C). Once the fraction of discriminators at the cooperator-discriminator equilibrium is low enough, defectors can invade and exploit the cooperators (Figure 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 (Figure 3A).

These considerations also explain why cooperation can be stabilized by information assortment (Figure 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 the section entitled Robustness.

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 (Figure 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 Figure 4B to Figure 4C). 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 Figure 4C to Figures 4D).

As we have seen above, in the absence of costs, increasing the probabilities p_o 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 discriminators to a stable interior equilibrium at which defectors are also present. A stable cooperator-discriminator equilibrium can then be recovered by increasing p_o 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 Figure 4C to Figure 4D). Details about these bifurcations are provided in the Supporting Information, Section S5.

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, Figures S4–S7). If a stable cooperator-discriminator 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 Figures 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 $p_c < 1$, so the boundaries of the dark-blue regions in Figures 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, Figures 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, Figures S5 and S7). In other words, parameter combinations a_{int} , a_{inf} , p_o , 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, Figures 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_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 Figures 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_t or p_o can turn a stable interior equilibrium into a neutral center. This is indicated by the white regions in the Supporting Information, Figure S8B,D.

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 group's 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 (Axelrod & Hamilton, 1981; Pepper & Smuts, 2002; Panchanathan & Boyd, 2004; Doebeli & Hauert, 2005; Fletcher & Doebeli, 2006; Nowak, 2006; Ackermann et al., 2008; Rankin & Taborsky, 2009; Ghang & Nowak, 2015; 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 (Nowak & Sigmund, 1998a,b; Panchanathan & Boyd, 2004; Brandt & Sigmund, 2006; Ohtsuki & Iwasa, 2006; Uchida & Sigmund, 2010; Nakamura & Masuda, 2011). In particular, our model reverts to that of Nowak & 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 & Doebeli, 2006) and to support the evolution of spite, an action that hurts both the actor and the recipient (West & Gardner, 2010; Smead & Forber, 2013; Forber & Smead, 2014). Negative assortment can also lead to a higher rate of conflict (Choi & 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 “green-beard” mechanism is known to give rise to positive assortment (Gardner & West, 2010; Nonacs, 2011) and to support cooperation (Nowak, 2006; Sinervo et al., 2006; Smukalla et al., 2008; Rankin & Taborsky, 2009; Gardner & West, 2010). 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 (Panchanathan & Boyd, 2004; Fletcher & Doebeli, 2006; Nowak, 2006). 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 & 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 & 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 Figures 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 Figure 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 (Nowak & Sigmund, 1998a,b; Brandt & Sigmund, 2006; Nakamura & Masuda, 2011). In particular, Nowak & 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 & 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 (Sims, 2003, 2006; Matejka & Sims, 2011; Caplin & Dean, 2015). 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 & 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 partner’s 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 cooperator-discriminator 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 & Kimura, 2013). In our model, making information more costly can destabilize otherwise stable cooperative equilibria. There is also a counter-intuitive 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 (Nelson, 1970; Waddington, 1985; Laughlin et al., 1998; Laughlin, 2001; MacIver et al., 2010; Caplin & Dean, 2015), 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 donor's reputation is updated does not depend on either his or the recipient's 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 & 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 agent's 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 & 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.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Highlights

- Cooperation can persist when individuals preferentially interact with individuals of other types.
- Cooperation can persist when individuals preferentially observe individuals of the same type.
- Increasing the available information can make it more difficult for cooperation to persist.
- When information is costly, cooperation based on indirect reciprocity is less stable.

Figure 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 $a_{\text{inf}} = a_{\text{int}}$. 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, although a neutral interior equilibrium exists. 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 purple region, there is a stable cooperator-defector equilibrium. In the phase portraits (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, saddles with half white and half black circles, and neutral centers with gray circles. Parameters: in B, $a_{\text{int}} = 0.93$, $a_{\text{inf}} = 0.93$; in C, $a_{\text{int}} = 0.98$, $a_{\text{inf}} = 0.98$; in D, $a_{\text{int}} = 1$, $a_{\text{inf}} = 1$; in E, $a_{\text{int}} = 1.005$, $a_{\text{inf}} = 1.17$; in F, $a_{\text{int}} = 1.24$, $a_{\text{inf}} = 1.17$; in all panels, $p_o = 0.85$, $p_r = 0.95$, $R = 10$, $b = 10$, $c = 1$, $p_c = 0.5$, and $s = 0$.

Figure 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_o of observing and p_r of remembering. The horizontal axis extends until $p_o = a_{\text{inf}}$, beyond which p_o 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 darkblue region, there is a stable cooperator-discriminator equilibrium. In the light-blue region, there is a stable equilibrium at which with 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, 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, and saddles with half

white and half black circles. Parameters: in B, $p_T = 0.25$, $p_0 = 0.3$; in C, $p_T = 0.6$, $p_0 = 0.3$; in D, $p_T = 1$, $p_0 = 0.3$; in all panels, $a_{\text{int}} = a_{\text{inf}} = 0.93$, $R = 10$, $b = 10$, $c = 1$, $p_c = 0.5$, and $s = 0$.

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Figure 3.

Increasing the probabilities p_o of observing or p_r of remembering can allow defectors to invade and decrease the probability of cooperation. In (A) and (C), 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_o and p_r , respectively. This is equivalent to taking a horizontal and a vertical path, respectively, through Figure 2A. In (B) 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_o 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 lines are shown for a particular value of p_o or p_r , no stable cooperative equilibrium exists for that value. Parameters: $p_r = 1$ (unless varied), $p_o = 0.3$ (unless varied), $a_{\text{int}} = a_{\text{inf}} = 0.93$, $R = 10$, $b = 10$, $c = 1$, $p_c = 0.5$, and $s = 0$.

Figure 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 $p_o = a_{\text{inf}}$, 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. Unstable equilibria are

indicated with white circles, 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, $p_o = 0.8$, $p_r = 0.9$, $a_{\text{int}} = a_{\text{inf}} = 1.01$, $R = 10$, $b = 10$, $c = 1$, and $p_c = 0.5$.