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Reciprocity evolves more readily in competitive than cooperative socio-ecologies

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Tracking what others did and matching other's expected actions is seen across a range of biological systems. As reciprocal matching rewards and reinforces cooperators and punishes and discourages non-cooperators, reciprocal matching can help communal living. The strength of reciprocity as a social strategy also comes from its success in protecting the individual against the risk of exploitation by punishing defectors. Although often overlooked, this feature carries a strong weight when exploitation risk is high. Here, we use evolutionary agent-based simulations to examine how reciprocal matching evolves across competitive socio-ecologies with a high risk of exploitation and cooperative socio-ecologies with a lower risk of exploitation. Results show that reciprocal matching as a social strategy for communal living evolves more readily in more competitive socio-ecologies where the risk of exploitation is high. Results also hold in standard Prisoner's Dilemmas with its equilibrium in single strategies (i.e. unconditional non-cooperation), for specific forms of reciprocity (i.e. tit-for-tat) and the likelihood of repeated interactions. Because reciprocal matching requires some capacity for social perception and memory, these findings suggest that such capacities for social cognition likewise serve to protect against exploitation and evolved in more competitive socio-ecologies as well.

1. Introduction

Reciprocity in social interactions is seen in a broad range of social species and biological systems [1–9]. Matching what others did or are most likely to do is common during cooperative interactions like gift exchange and food sharing [10–12], and observed during conflict—an eye for an eye, a tooth for a tooth [13–15]. Sometimes intentional and strategic, for example, to secure agreement and to avoid losing conflict [16], reciprocal matching often appears automatic and outside of the individual's control. Indeed, reciprocal interactions are supported by interpersonal synchronizations in the release of hormones like oxytocin [17–19], heart rate [20,21] and facial expressions [22,23]. Furthermore, as a social strategy for communal living, reciprocal matching often outperforms alternative strategies for cooperation, especially unconditional strategies that do not consider partner interaction histories and reputations [10,24–26].

Reciprocal matching is seen across a range of animal species and for a variety of tasks (table 1). Behavioural matching of cooperation is documented, for example, in hermaphrodite worms [27,28], in several fishes [29–31] and birds [32–34] and in a range of mammalian species [11,35–50]. It happens during joint predator inspection [29], sentineling and giving support during third-party aggression [31,36,43], digging joint shelter [30], food provisioning

[31,35,38,39,45,47,48], alliance formation and movement [34,37], (allo)grooming [42–44] and, in humans, financial exchange [11,48–50] (for reviews see [51–56]). At the same time, while these manifestations of reciprocal matching might be more relevant in specific socio-ecologies, where and how reciprocal matching evolved remains unspecified. Prevailing theory and research in the biobehavioural sciences proceed by assuming that altruistic behaviour can be favoured by natural selection if the fitness effects of the actor and receiver are somehow positively correlated [9]. Such correlation can come about by an above-random chance that helping someone increases the likelihood of receiving help back [57–59], and that not helping increases the likelihood of not receiving help back—through reciprocal matching partners reward cooperation and punish non-cooperation with defection [24,60].

Past research often examined the evolution of reciprocal matching in the standard Prisoner's Dilemma. As this provides a context in which the benefits of rewarding cooperation and punishing defection cannot be easily distinguished [61], we presently poorly understand the value of reciprocity across socio-ecologies that vary in terms of the relative importance of rewarding cooperation or punishing defection. Here, we address this open issue with game-theoretic analyses of socio-ecologies and evolutionary agent-based simulations. We show that reciprocal matching emerges especially when socio-ecologies involve higher risk of exploitation (i.e. situations where an agent defects when partner cooperates). Our findings suggest that even simple forms of social memory and perception gain in relevance in more competitive socio-ecologies [62].

(a) When Rousseau meets Hobbes

Social interactions often confront individuals with a choice between cooperating and not cooperating. When cooperating is individually costly yet benefitting others, unconditional cooperation can be individually risky, as it can be exploited by free-riders. In the standard Prisoner's Dilemma, for example, non-cooperation (as an alternative to cooperation) serves the individual's interests to gain competitive advantage and to punish other's defection [24,25,61,63,64]. When interactions repeat, however, reciprocal strategies are more likely to evolve because they reward past cooperation, and punish past non-cooperation [24,58,65] (but see [66]).

What often goes unnoticed is that reciprocity—cooperate when the other cooperated, otherwise refrain from cooperating—cannot only be relevant in situations that rewards cooperation and deters non-cooperation, but also in situations where the risks of exploitation and the deterrence of non-cooperation become more prominent. Such risk of exploitation depends, in turn, on the socio-ecology within which interactions take place [67]. For example, in the peaceful state of nature proposed by the philosopher Jean-Jacques Rousseau, individuals are most likely to interact with those for whom reciprocal helping is in their best interest [9,59,68,69]. Conversely, in the war-like state of nature hypothesized by Thomas Hobbes [70–72], individuals more likely encounter partners for whom exploiting cooperators is in their best interest (*viz.* anti-reciprocity [73]). Compared with Rousseauian ecologies, the need to track others' reputations and to punish defection is comparatively high in Hobbesian ecologies. This means that adaptive strategies for cooperation and conflict based on (in)direct reciprocity may be more (or less) relevant across different socio-ecologies that vary on their need to reinforce cooperation or to punish defection.

To examine these possibilities, we modelled socio-ecologies in terms of the games individuals most likely play when interacting. With its simple and standardized models of interaction strategies and their payoff consequences [74–77], game theory offers a range of models that can capture distinct properties of socio-ecologies and in particular how interacting individuals' interests are related and affected by their individual decisions to cooperate or not [78]. The game of Stag Hunt, for example, models the Rousseauian peaceful state of nature [71]. Unlike the Prisoner's Dilemma, where defection is the strictly dominant strategy because it yields a higher payoff regardless of the opponent's choice (figure 1a), Stag Hunt has two pure equilibria—cooperate when the other cooperates and defect when the other defects—and a mixed-strategy equilibrium, and interacting individuals can gain some individual resources by non-cooperating but gain more through mutual cooperation (figure 1b). Because exploiting other's cooperation brings no personal advantage, the risk of exploitation—and the need to protect (i.e. deter non-cooperation)—is low [68,79–81]. This is different in the game of Chicken, which models the Hobbesian war-like socio-ecology (figure 1c). In the game of Chicken, and similar games like Hawk Dove and Snowdrift, there is an equilibrium in mixed strategies and two pure equilibria (compete when the other cooperates, cooperate when the other competes). Interacting individuals can safely gain some resources from reciprocal cooperation, but each of them would be better off by exploiting the other party's cooperation through non-cooperation (anti-reciprocity [82,83]). Accordingly, in the game of Chicken, the risk of exploitation is comparatively high.

To study the evolution of adaptive strategies across socio-ecologies that differ in competitiveness we varied the prevalence of types in a population of fixed size. We have two types of agents, Rousseauian and Hobbesian, each defined by the individual's payoffs from the possible combinations of actions they and their partner take (CC, CD, DC, DD), where C stands for cooperation and D for defection. A Rousseauian type earns most from mutual cooperation (CC or reward payoff R), followed by unilateral defection (DC or temptation payoff T), mutual defection (DD or punishment payoff P) and by unilateral cooperation (CD, or sucker payoff S). A Hobbesian type earns the most from unilateral defection, followed by mutual cooperation, unilateral cooperation and mutual defection. Types can randomly meet with other types. When a Rousseauian meets a Rousseauian, they are in Stag Hunt (figure 1b) and when a Hobbesian meets another Hobbesian, they interact in Chicken (figure 1c). In our set-up, however, Rousseauians can also meet Hobbesians. If this happens, they interact in a game of Attack–Defend (figure 1d). Here, for Rousseauians playing D protects against exploitation by the Hobbesian partner playing D too, akin to a defend–attack interaction. Playing D is costly, however, when the Hobbesian partner played C. Differently put, the attack–defend game played when Rousseauians meet Hobbesians has a unique equilibrium in mixed-strategies [84,85]. Anti-reciprocity—compete when the other cooperates, otherwise cooperate—is in the best interest of the Hobbesian player (as in the game of Chicken)

Table 1. Behavioural manifestations of reciprocal matching across animal species and tasks. Examples show how interacting individuals take their partner's history of cooperation into account when cooperating themselves. Listed examples could exclude alternative mechanisms like kin-selection, co-action or mutualism. The listing reveals that reciprocal matching can happen but remains agnostic to the prevalence or robustness of behavioural reciprocity as a social strategy within or across animal species and socio-ecologies.

species	behavioural manifestation of direct reciprocity
non-vertebrates	
hermaphrodite worms	**egg-laying**: in isolated dyads of hermaphroditic polychaete worms (*Ophryotrocha diadema*), individuals engage in iterated exchanges of eggs for sperm (eggs are a costly donation relative to sperm); if a partner donates eggs and the other fertilizes them, the latter is likely to donate eggs a couple of days later [27,28]
vertebrates	
fishes	
guppies	**predator inspection**: female guppies (*Poecilia reticulata*) disproportionately engaged in predator inspection with others with whom they cooperated before [29]
cichlids	**shelter digging**: cichlids (*Neolamprologus pulcher*) in dyads dig out a joint shelter; digging efforts increased when a social partner had helped to dig out the common shelter in a previous time period [30]
teleost fishes	**foraging/sentineling**: pairs of coral reef rabbitfishes (f. Siganidae) create a balanced distribution of foraging activity by alternating in taking an upright vigilance position allowing the partner to forage in small crevices in the reef substratum [31]
birds	
great tits	**alloparenting**: great tit (*Parus major*) parents raising chicks together alternated visits to the nest more than would be expected by chance, speeding up their feeding rate after their partner had visited the chicks and slowing down again once they had visited in turn [32]
ravens	**memory for fair treatment**: ravens (*Corvus corax*) in an exchange paradigm could exchange a low-quality for a high-quality food item and remember who, on a previous occasion, was a reliable 'fair' experimenter and who would not reliably exchange (the 'unfair' experimenter)—ravens chose to interact with the former [33]
ibis	**V-flight formation**: the time an individual is leading a formation of juvenile orthern bald ibis (*Geronticus eremita*) is correlated with the time the individual profits from flying in the wake of another bird; birds match the time they spend in the wake of each other by frequent pairwise switches of the leading position [34]
mammals	
bats	**food sharing**: common vampire bats (*Desmodus rotundus*) sharing blood with non-kin expands the number of possible donors beyond kin and promotes reciprocal help [35]
ring-tailed Coati	**support during aggression**: ring-tailed coati (*Nasua nasua*), a social carnivore, reciprocally support each other in consecutive aggressive conflicts independent of spatial association and subunit membership [36]
bottlenose dolphins	**alliance formation**: male bottlenose dolphins (*Tursiops truncatus*) in pairs or trios of unrelated males cooperate to herd individual females; behavioural data combined with sound playback experiments show that males form a first-person social concept of cooperative team membership [37]
Norway rats	**food provisioning**: Norway rats (*Rattus norvegicus*) encountered four different partners that were either helpful or not, on four consecutive days; on the fifth day, the focal subject was paired with one of the previous four partners and given the opportunity to provide it with food; the focal rats returned received help by matching the quantity of help their partner had previously provided [38,39]
capybara	**token exchange**: four capybaras (*Hydrochoerus hydrochaeris*) chose between a prosocial token that rewarded themselves and a recipient, a selfish token that only rewarded themselves, and a null token that provided no reward to anyone; results indicated direct reciprocity, with capybaras being more likely to be prosocial towards a prosocial recipient [40]
reindeer	**allonursing**: semi-domesticated reindeer (*Rangifer tarandus*) mothers increased allonursing as a function of help received from their partner and the overall number of help received [41]
meerkats	**grooming**: In groups of the cooperatively breeding meerkat (*Suricata suricatta*), groomees returned grooming of the groomer within the grooming bout more frequently [42]
dwarf mongooses	**grooming/sentineling**: in wild dwarf mongooses (*Helogale parvula*), group members who contributed more to sentinel behaviour received more grooming later that day [43]
vervet monkeys	**grooming for tolerance**: low-status vervet monkeys (*Chlorocebus pygerythrus*) trade grooming for short-term tolerance by dominant conspecifics [44]
orangutans	**token-exchange**: two orangutans (*Pongo pygmaeus abelii*) could exchange a token for food with the experimenter, but only after first obtaining the token from the other orang-utan; towards the end of the study, orang-utans reciprocally exchanged (mainly partner-valuable) tokens both between and within trials [45]

(*Continued.*)

Table 1. (*Continued.*)

species	behavioural manifestation of direct reciprocity
Guinea baboons	**gift exchange**: guinea baboons (*Papio papio*) can use direct reciprocity and partner choice to develop and maintain high levels of cooperation in a prosocial choice task [46]
chimpanzees	**helping to food provision**: chimpanzees (*Pan troglodytes*) could help a partner to obtain a tool for accessing a reward; chimpanzees showed a higher tendency to help when interacting with a helpful compared with an unhelpful partner only in the first half the experiment [47,48]
humans	**gift exchange**: in economic games of trust, humans (*Homo sapiens*) in the role of investors donated more to a recipient, who in turn returned more than what each should give from a strict payoff maximization perspective (i.e. zero) [11,49,50]

and reciprocity—compete when the other competes, otherwise cooperate—is the Rousseauian's best interest (as in Stag Hunt) [58,86].

(b) Modelling the competitiveness of socio-ecologies

Socio-ecologies that include Hobbesian types are more competitive—risk of exploitation increases—than those that include Rousseauians only. If reciprocity is mostly effective in socio-ecologies where it rewards cooperators and punishes non-cooperators, we would see reciprocity outperform unconditional cooperation and defection in Rousseauian socio-ecologies, where interactions take place in Stag Hunt. If reciprocity is particularly prominent in socio-ecologies where the risk of exploitation is high, we would see it outperforms unconditional strategies, especially in more competitive socio-ecologies, where interactions take place in Chicken games. To examine these possibilities, we scaled the competitiveness of the socio-ecology by creating five populations (figure 2): Rousseauian only (100% Rousseauian), Rousseauian majority (75% Rousseauian, 25% Hobbesian), equal proportion (50% Rousseauian, 50% Hobbesian), Hobbesian majority (25% Rousseauian, 75% Hobbesian), Hobbesian only (100% Hobbesian). Accordingly, a *Rousseauian-only* system is characterized by cooperative social interactions (Stag Hunt only; figure 2a), while a *Hobbesian-only* socio-ecological system is characterized by competitive social interactions (Chicken only; figure 2b). Mixed populations are taking an intermediate position in terms of the competitiveness and include attack–defend interactions whenever Hobbesians meet Rousseauians (figure 2c–e).

2. Results and methods

(a) Interaction strategies and payoffs

Assuming that agents do not learn about their partner's strategy and past behaviour, the three games in our analysis—Stag Hunt, Chicken and Attack–Defend—all share the same mixed-strategy Nash equilibrium (0.5, 0.5), meaning that if one player randomizes between cooperation and non-cooperation with equal probability, then there is no strategy that can outperform randomization. Yet with information about the partner, random mixing may be inferior to alternative 'reactive' strategies that are defined by (i) what an agent does in the initial round, (ii) what an agent does when the partner cooperated before, and (iii) what an agent does when the partner defected before. For our analysis, we thus have three unconditional and two conditional strategies (table 2).

Because all three games we use have similar structures, we use the same notation for the payoffs as above, although the actual payoff values differ in each game. We denote the payoff of mutual cooperation with R, mutual defection with P, the payoff of defection against cooperation with T and the payoff of cooperation against defection with S. We can then calculate the payoff for each of our five strategies against each other strategy (see table 3). For the repeated supergame, we assume that agents play the first round with probability 1 and for the rest, they continue to interact with probability δ, such that games continue for an average of $1/(1-\delta)$ rounds. Parameter δ can be a prominent factor for the evolution of cognitively sophisticated strategies, such as match and mismatch [24].

We note that in all three games, each type's own payoff remains consistent across the games they participate in. Thus, while payoffs do not vary between partners, the composition of partner distribution (and therefore the type of games agents are embedded in) differs under distinct ecological conditions (i.e. population compositions). For a full breakdown of this analysis, see §2 in electronic supplementary material.

In our model, a Rousseauian type earns 2 (CC), 0 (CD), 1 (DD) or 1 (CD) and Hobbesian player earns 1 (CC), 1 (CD), 2 (DC) or 0 (DD). Here, choosing C earns the Rousseauian 2 or 0 when the Hobbesian partner, respectively, plays C (and earns 1) or D (and earns 2). Choosing D, in contrast, earns the Rousseauian player 1 both when the Hobbesian partner plays C (and earns 1 also), or D (and earns 0). Assuming these payoffs, we can derive the payoff for Rousseauian and Hobbesian players as a function of strategy pairing and repetition probability $\delta = 0.6$, 0.8 and 0.99 (figure 3) (formal derivations for the full parameter space are given in §2 of electronic supplementary material). This shows the fitness functionality of different strategy pairings for Rousseauian and Hobbesian types, with the former generally benefitting more from mutual cooperation and matching and the latter benefitting more from exploitation (defect when partner cooperates), mismatching (cooperate when partner defects) and mutual defection.

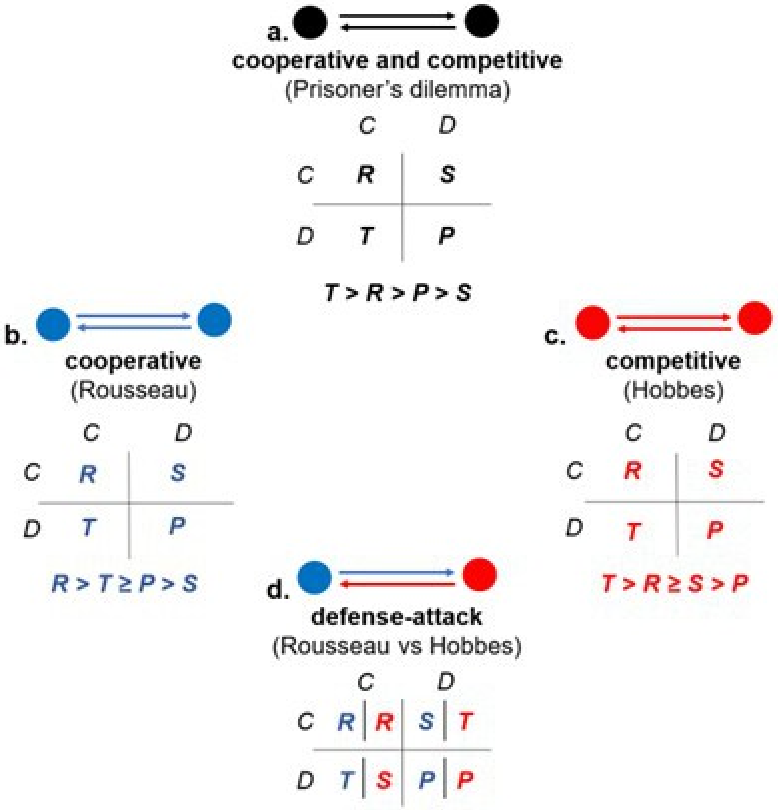

Figure 1. Variation in social interactions. The plot shows the incentive structure of different 2×2 game models from the perspective of the row player, where each cell represents the payoff received depending on both players' choices. In each game, individuals can choose between cooperating (*C*) or defecting (*D*). They model mixed-motive social interactions ((a) Prisoner's Dilemma), cooperative environments ((b) Stag Hunt; conflict between safety and cooperation), competitive environments ((c) Chicken; conflict between safety and competition) and their combination ((d) Attack–Defend; asymmetric conflict between competition and safety). T = temptation payoff, R = reward payoff, S = Sucker payoff, P = punishment payoff.

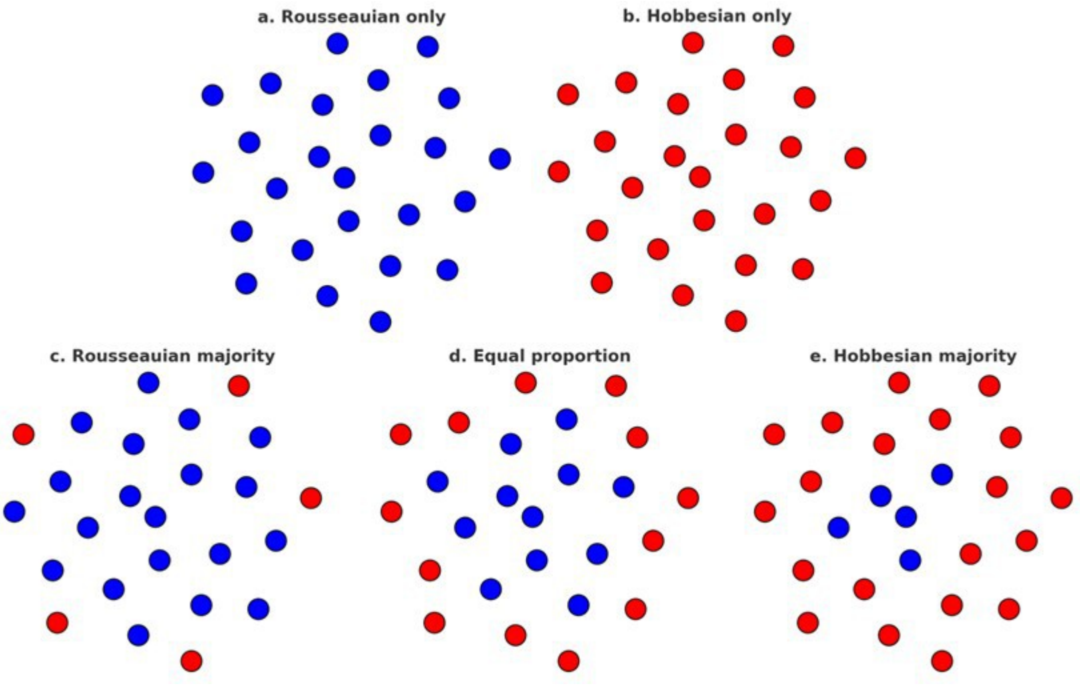

Figure 2. Socio-ecological systems. Graphic visualization of the distribution of types across the five populations $N_T = 240$ agents yielding different levels of socio-ecological competitiveness (from lowest in Rousseauian only, to highest in Hobbesian only). In a socio-ecological system characterized by Rousseauian types only (a), agents only interact in Stag Hunt games. In a socio-ecological system characterized by Hobbesian types only (b), agents only interact in Hawk Dove games. In the remaining socio-ecological systems where Hobbesian types can meet Rousseauian types (c–e), agents can interact in an Attack–Defend game. While in the Rousseauian majority there is a prevalence of Stag Hunt games (c), in the Hobbesian majority there is a prevalence of Hawk Dove games (e).

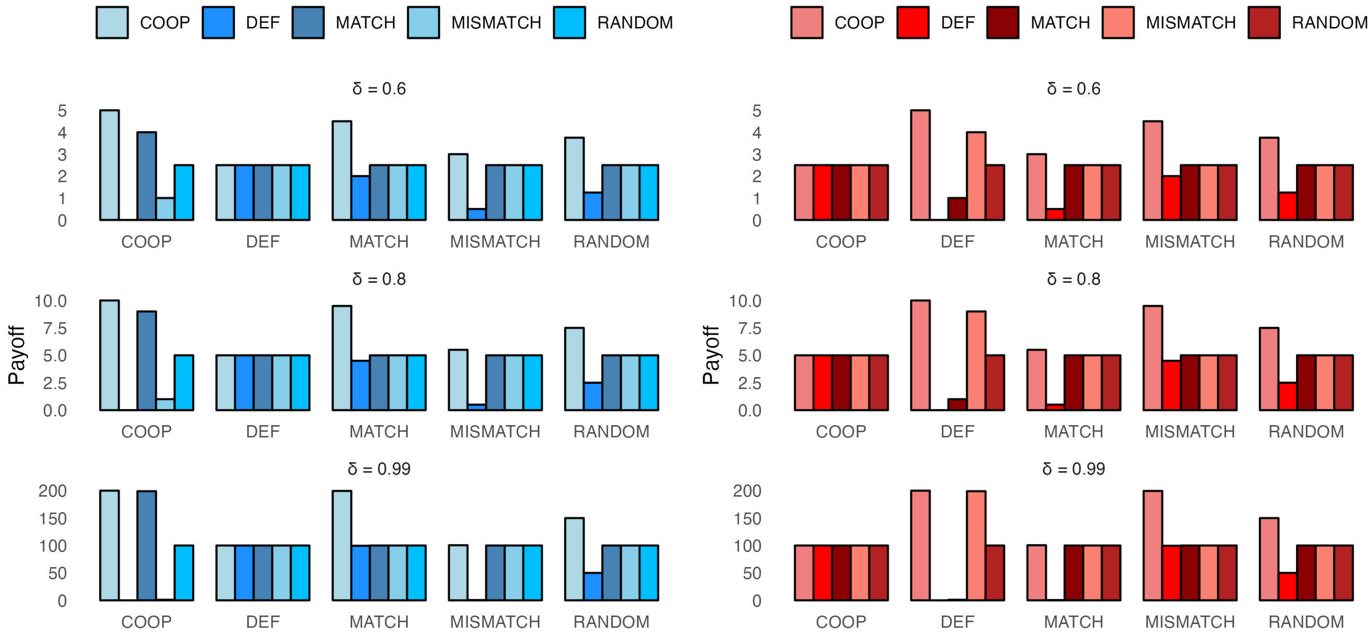

Figure 3. Repeated game payoffs for Rousseauian (blue) and Hobbesian (red) players under various strategy combinations and for different probabilities of repetition (a,b: $\delta = 0.6$; c,d: $\delta = 0.8$; e,f: $\delta = 0.99$). Each value (y-axis) represents the expected payoff of a strategy (x-axis) against another strategy (colour) in the repeated game when there are no mistakes.

Table 2. List of strategies considered in the simulations. Note: matcher strategy is similar to the common tit-for-tat strategy. The only difference is that tit-for-tat starts with cooperation.

strategy	behaviour
random	starts with either cooperation or defection with equal probability, and randomly chooses to cooperate or defect in all rounds
cooperator	starts with a cooperation and always cooperates, regardless of the partner's action
defector	starts with a defection and always defects, regardless of the partner's action.
matcher	starts with either cooperation or defection with equal probability, and cooperates in the following round if the partner cooperates, and defects in the following round if the partner defects
mismatcher	starts with either cooperation or defection with equal probability, and defects in the following round if the partner cooperates and cooperates in the following round if the partner defects

Table 3. General form of the repeated game payoff for the strategies where R denotes the payoff for mutual cooperation, P denotes the payoff for mutual defection, T denotes the payoff for defection when the partner cooperates, and S denotes the payoff for cooperation when the partner defects in the stage game.

	cooperation	defection	match	mismatch	random
cooperation	$\frac{R}{1-\delta}$	$\frac{S}{1-\delta}$	$\frac{1}{2}\left(S+\frac{R(1+\delta)}{1-\delta}\right)$	$\frac{1}{2}\left(R+\frac{S(1+\delta)}{1-\delta}\right)$	$\frac{R+S}{2(1-\delta)}$
defection	$\frac{T}{1-\delta}$	$\frac{P}{1-\delta}$	$\frac{1}{2}\left(T+\frac{P(1+\delta)}{1-\delta}\right)$	$\frac{1}{2}\left(P+\frac{T(1+\delta)}{1-\delta}\right)$	$\frac{P+T}{2(1-\delta)}$
match	$\frac{1}{2}\left(T+\frac{R(1+\delta)}{1-\delta}\right)$	$\frac{1}{2}\left(S+\frac{P(1+\delta)}{1-\delta}\right)$	$\frac{1}{4}\left(\frac{P+R+S+T}{1-\delta}\right)$	$\frac{1}{4}\left(\frac{P+R+S+T}{1-\delta}\right)$	$\frac{1}{4}\left(\frac{P+R+S+T}{1-\delta}\right)$
mismatch	$\frac{1}{2}\left(R+\frac{T(1+\delta)}{1-\delta}\right)$	$\frac{1}{2}\left(P+\frac{S(1+\delta)}{1-\delta}\right)$	$\frac{1}{4}\left(\frac{P+R+S+T}{1-\delta}\right)$	$\frac{1}{4}\left(\frac{P+R+S+T}{1-\delta}\right)$	$\frac{1}{4}\left(\frac{P+R+S+T}{1-\delta}\right)$
random	$\frac{R+T}{2(1-\delta)}$	$\frac{P+S}{2(1-\delta)}$	$\frac{1}{4}\left(\frac{P+R+S+T}{1-\delta}\right)$	$\frac{1}{4}\left(\frac{P+R+S+T}{1-\delta}\right)$	$\frac{1}{4}\left(\frac{P+R+S+T}{1-\delta}\right)$

(b) Simulations

To handle the complexity of our setup, multiple fixed socio-ecologies involving multiple types and strategies for each type, and account for randomness such as mistakes and mutation, we take a computational approach. We used simulations to examine when and to what extent each of the five strategies evolves across the five different socio-ecologies and with different probabilities of repeated interactions with $0.6 \leq \delta \leq 0.99$ (results are also robust when using a replicator dynamics approach, see electronic supplementary material, §2).

At the beginning of each simulation, we generate two fixed-size populations of agents that can interact with each other—one population for *Rousseauians* and one population for *Hobbesians*. Naturally, we have a single population in *Rousseauian-only* and

Hobbesian-only conditions. We randomly assign to each agent one of the strategies selected from our set of five with equal chances (see §2b), randomly pair them up with another agent and implement the interaction strategy.

Agents play the first round of the game with certainty, and they play each subsequent round with probability δ. To determine the number of rounds that agents play with each other in our simulations, we used a geometric distribution with the parameter $p = 1 - \delta$ (with $0.6 \le \delta \le 0.99$, per the above). Agents' payoffs are accumulated over all rounds of the interaction. At the end of all interactions in the generation, we compute each agent's relative payoff in their population as follows:

$$f_i = \frac{x_i}{\sum_{j=1}^{N_k} x_j}(1 - s) + s,$$

where x_i is the total payoff of agent i from the interactions, N_k is the number of agents in the population k (*Rousseauian* or *Hobbesian* population) and s is the base fitness parameter, with $s \in [0,1]$. Base fitness determines how strongly the payoffs affect fitness, and a lower base fitness, represents a higher intensity of selection. When the base fitness is 0, an agent's probability of replacing itself in the next generation (in terms of the strategy the agent uses) is directly the relative payoff of the agent within the population. If the base fitness is 1, each strategy would have an equal chance to be replaced in the next generation regardless of the payoffs. In other words, a higher base fitness gives a symmetric chance to all strategies. We used a base fitness of 0.01 (with population $N_T = 240$), and we ran the simulations with a base fitness of 0.1 as a robustness check (see electronic supplementary material, figure S12 in §III).

An agent might live a single generation or longer depending on random replacement. At the beginning of the new generation, all payoffs were set back at 0 and we repeated the process for 1000 generations. Across generations, we kept the percentage of types in a population constant and replaced strategies using a stochastic reproduction process. We assume that a fraction of agents die (or learn) in each generation and each one is replaced by another agent (or change strategy after learning), proportional to the relative payoffs of the agents at the end of the previous generation. We used a replacement rate of 50% and we further ran the simulations with a replacement rate of 100% as a robustness check (see electronic supplementary material, figure S13). A higher replacement rate represents a faster speed of the evolutionary process.

In our simulations, we allowed for random mutations in each agent's strategy with probability μ ($\mu = 0.001$ with population $N_T = 240$; see electronic supplementary material, figure S14 in §III for a robustness check with $\mu = 0.01$). In addition, we considered that agents make mistakes, i.e. they respond with a random action (C or D) instead of responding with the designated action based on their strategy. The probability of making such a mistake is $\varepsilon = 0.005$ (with population $N_T = 240$; see electronic supplementary material, figure S15 for a robustness check with a mistake rate of $\varepsilon = 0.05$).

We performed 1000 independent simulations for each parameter combination. Results are based on the aggregate of 1000 independent iterations for each parameter combination (examples of individual iterations can be found in electronic supplementary material, figures S1–S6). Simulations were conducted in Python with a custom software implemented on the High Performance Computing cluster from the Academic Leiden Interdisciplinary Cluster Environment (ALICE) at Leiden University.

(c) Evolution of strategies when socio-ecologies differ in competitiveness

Results show substantial variation in the relative importance of strategies dependent on whether an individual is in a fully cooperative or competitive ecology. In the Rousseauian only socio-ecological system, being a cooperator is always the best strategy for the explored range of continuation probability ($0.6 \le \delta \le 0.99$). The benefit of such a strategy increases when more opportunities for direct reciprocity occur. Adaptive strategies, such as match and mismatch, are not successful in cooperative environments (figure 4a). By contrast, in a fully competitive environment, the set of adaptive strategies is dramatically different. First, in such environments, repeated interactions favour defectors over cooperators. Moreover, mismatching what the partner did in the previous round (anti-reciprocity) is always more successful than any other strategy (figure 4b).

In a subsequent analysis, we considered the three socio-ecological systems with intermediate competitiveness (Rousseauian majority, equal size, Hobbesian majority). Whereas a small fraction of competition (25% of Hobbesian types) does not successfully disrupt the value of pure cooperation strategies among Rousseauians (bottom panel in figure 5a), the success of pure cooperation for Rousseauians collapses in favour of more sophisticated matching strategies when Hobbesian types become more prevalent, and the likelihood of both symmetric (Chicken) and asymmetric (Attack–Defend) competition increases (bottom panels in figure 5b,c). Accordingly, as the competitiveness of the socio-ecology increases, reciprocal strategies effectively protect Rousseauians against exploitation, especially as the number of repeated interactions increases (bottom panels in figure 5a–c). At the same time, we see that for Hobbesian types, mismatching (anti-reciprocity) is always performing better than any other strategy (top panels in figure 5a–c). Results generalize across continuation probabilities ($0.6 \le \delta \le 0.99$; figure 5a–c), mutation rates, mistake rates and base fitness and population sizes ($N_T = 60, 120, 240$) (§III in electronic supplementary material).

(d) Reciprocal matching in socio-ecologies with varying competitiveness

Earlier work on the evolution of cooperation afforded a strong role to reciprocity [24,25,58,63]. Here, we show that reciprocity is particularly valuable in competitive socio-ecologies, where it helps to counter exploitation. Earlier work considered one specific form of reciprocal matching, however, that begins with C and then matches the partner's previous action ('tit-for-tat' [84]).

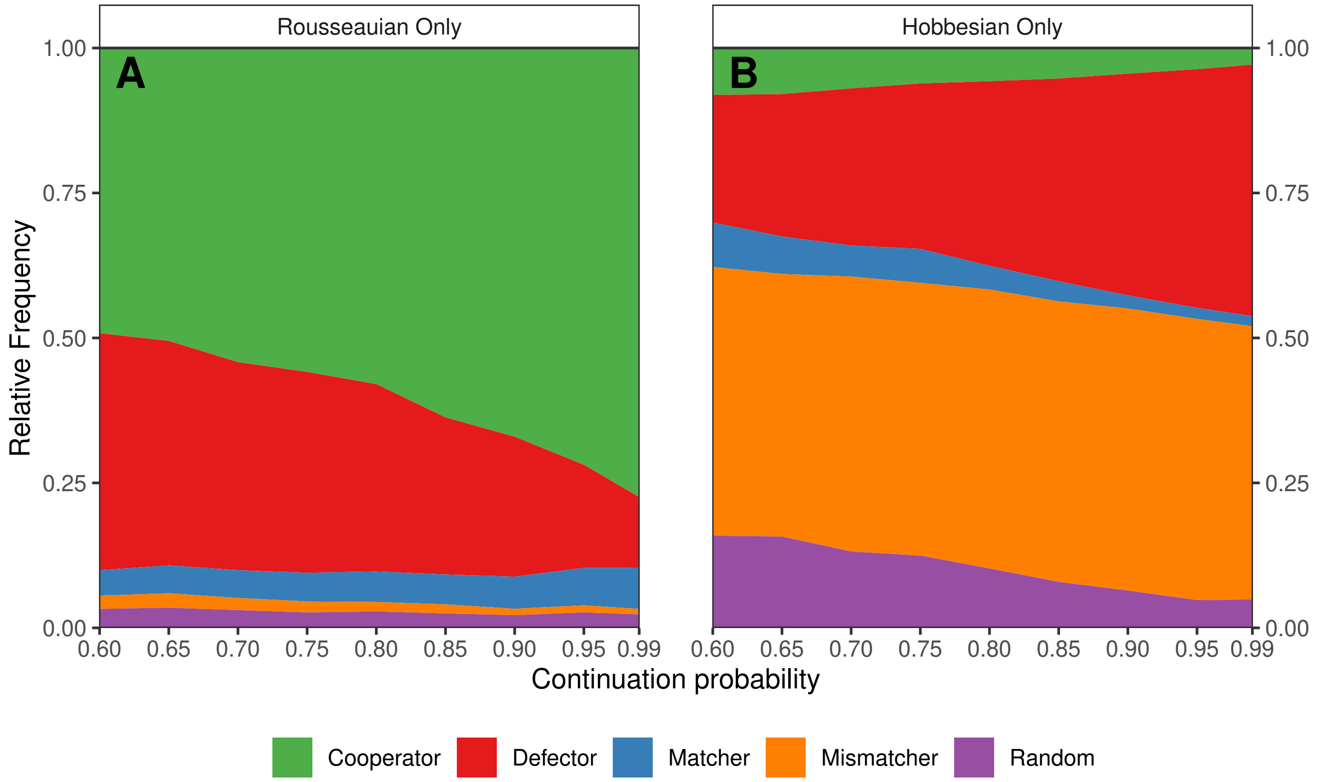

Figure 4. Relative success of strategies in cooperative and competitive environments. The plot shows the average frequency of agents with a certain strategy in Rousseauian-only (a) and Hobbesian-only (b) populations across continuation probabilities (*x*-axis). For each continuation probability, each point is the average frequency of a strategy across 1000 generations and 1000 simulations. A definition of each strategy is presented in table 2.

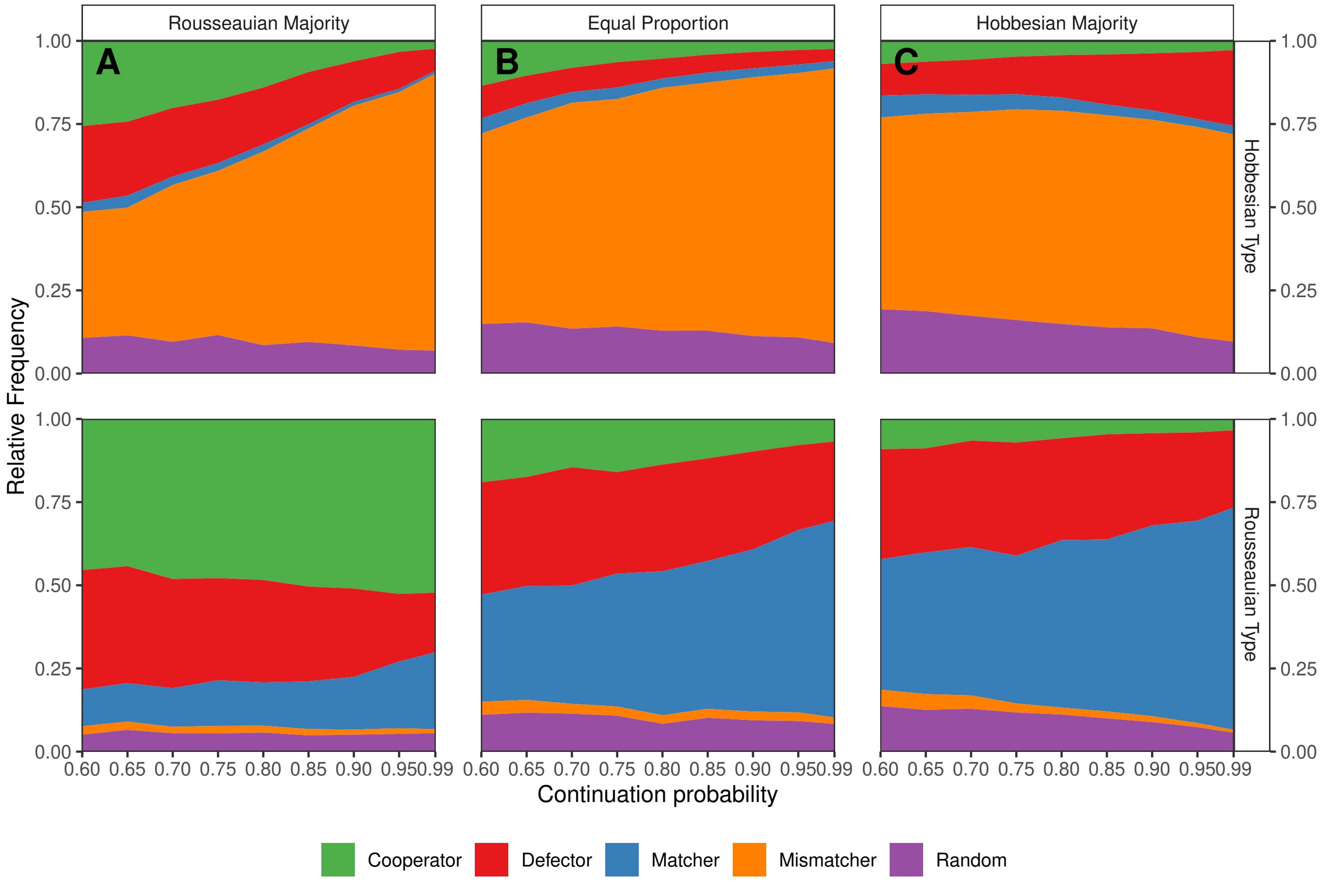

Figure 5. Relative success of strategies across mixed environments. The plot shows the average frequency of a strategy across three ecologies: Rousseauian majority (a), equal distribution (b) and Hobbesian majority (c). The *x*-axis represents different continuation probabilities. For each continuation probability, each point is the average frequency across 1000 generations and 1000 simulations.

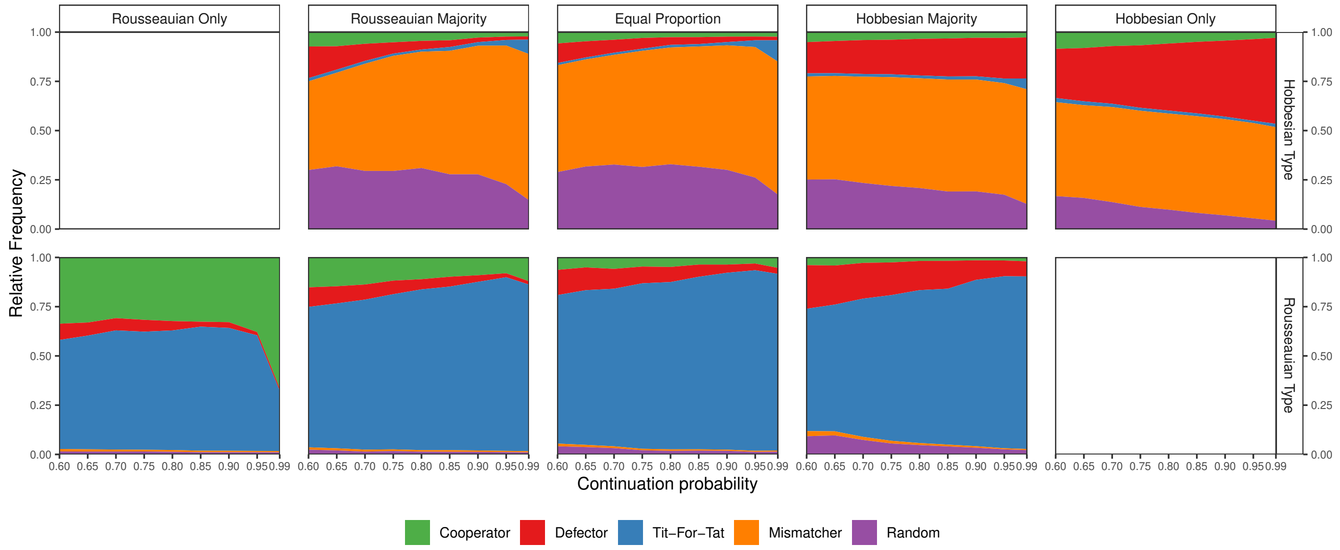

Figure 6. Relative success of tit-for-tat as a specific form of reciprocal matching across socio-ecologies varying in competitiveness. The plot shows the average frequency of agents with a certain strategy in different populations across continuation probabilities. For each continuation probability, each point is the average frequency of a strategy across 1000 generations and 1000 simulations.

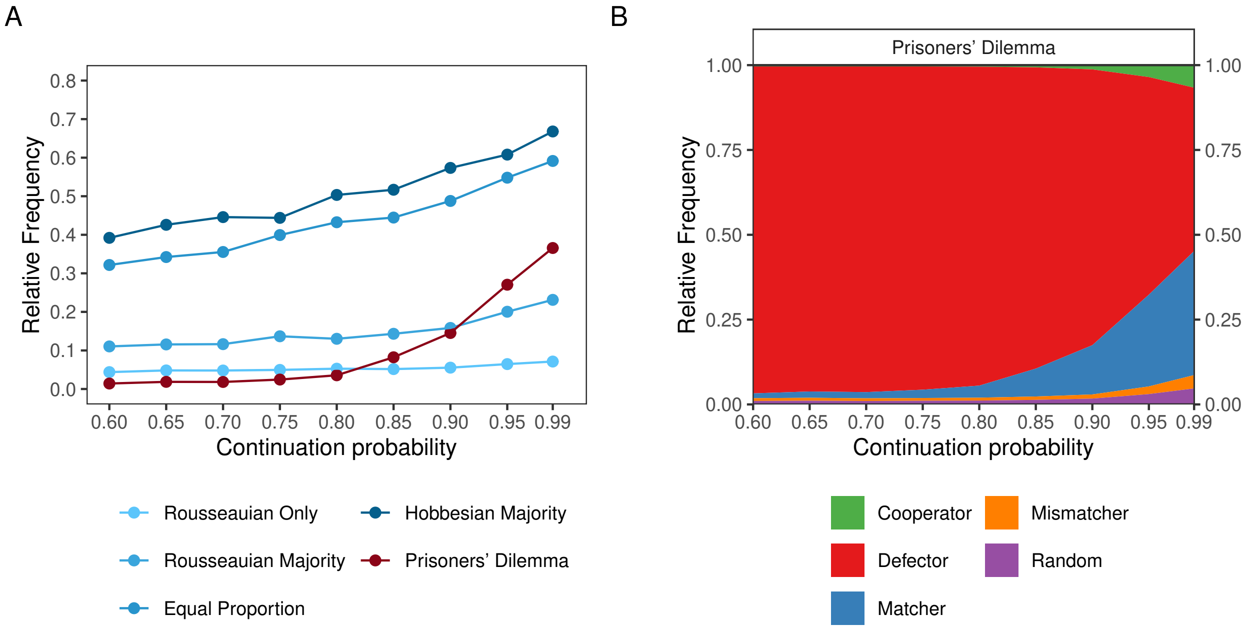

Figure 7. Reciprocity and the Prisoner's Dilemma. The plot shows the success of match strategies across continuation probabilities and population compositions when matching can be used as a means to defend from aggression (Rousseauians), compared with the success of matching strategies in the standard Prisoner's Dilemma game. The blue lines represent the success of matching strategies among Rousseauians in socio-ecological systems characterized by a certain degree of conflict with Hobbesians. Darker blue lines represent ecologies with a higher prevalence of asymmetric conflict and need to defend from defection, while lighter blue lines represent a lower prevalence of asymmetric conflict. The red line shows the success of matching strategies in the Prisoner's Dilemma game (see electronic supplementary material, (a). The plot shows the average frequency of agents with a certain strategy in different populations across continuation probabilities in the Prisoner's Dilemma (b).

However, when we replaced *Match* that begins with a random choice between cooperate and non-cooperate with tit-for-tat, which begins with cooperate, we see that also tit-for-tat is likewise successful especially when the fraction of Hobbesian agents increases (lower panels in figure 6). Tit-for-tat proves to be more successful than matching in Rousseauian-only environments, suggesting that starting with cooperation can boost the effectiveness of reciprocity across socio-ecologies.

Another possible explanation for the seeming discrepancy between our results and earlier work may be that we excluded the standard Prisoner's Dilemma from the set of games agents played. To verify this, we compared the relative success of match strategies among Rousseauians with the evolution of match strategies in the standard Prisoner's Dilemma game. When we computed the same set of simulations and set of strategies in the standard Prisoner's Dilemma game (PD, payoff matrix shown in figure 1a), we observed that a match strategy more readily evolves among Rousseauians that have high pressure to defend from exploitation in competitive environments (i.e. a large faction of Hobbesians), rather than in the Prisoner's Dilemma game (figure 7). Our results thus confirm that reciprocity promotes cooperation, yet that reciprocity evolves more readily in environments presenting a high need to defend against aggression.

3. Conclusions

The evolution of strategies for competition and cooperation depends on the socio-ecology within which individuals interact. Variations in socio-ecologies allow for trust or, alternatively, input a need to punish potential defection and through these variations, strategies that require some cognitive sophistication emerge. Indeed, socio-ecologies in which mutual cooperation is in the individual's best interest (i.e. Stag Hunt games) allow for pure cooperation to evolve, whereas socio-ecologies in which defection best serves personal interests (e.g. Prisoner's Dilemma games) afford pure competition and reciprocity to evolve. However, cognitively sophisticated strategies that take the history of play for cooperation or competition into account emerge as a function of the number of agents that seek to exploit through defection, and matching other's defection becomes crucial for the evolution of reciprocity.

Our finding that some socio-ecologies favour more cognitively sophisticated strategies nicely scales with the presence of multiple equilibria in which fitness depends on the strategy chosen by one's counterpart, and individuals benefit from an ability to track what others did and predict what others will do. Indeed, in the type of sequential encounters modelled here, direct reciprocity requires individual recognition and memory of the outcomes of past interactions with a specific individual. For indirect reciprocity, individual recognition of social partners as well as a reputation mechanism based on the performance of social partners is needed. Our results thus suggest that a species' cognitive sophistication may be a product of evolutionary pressure to deal with mixtures of competition and cooperation [84], and in particular in socio-ecologies where the temptation to defect is stronger. Results of these models resonate with recent calls for considering reciprocity across socio-ecologies [62], and are in line with cross-societal findings in human that show that forms of reciprocity are more prevalent in societies characterized by internal history of competition [85,87].

While our results provide reliable evidence that competitive environments promote reciprocal strategies in a controlled setting, they rely on a subset of relatively simple strategies and assumptions, whereas the literature on game theory has a wide range of prolific strategies and parameters [24,88]. Future research is needed to extend the present findings to a more diverse set of strategies (including Generous TitForTat, GrimTrigger, WinStayLoseShift or generalized reciprocity [72,89]) and parameters (including population structure, or multi-level fitness benefits [24,90]). Whether different kinds of reciprocal strategies are also more pronounced in more competitive settings should be further investigated in the presence of such an extended set of strategies.

Social animals experience a wide set of social interactions across ecologies, and across animal species and ecologies, there is evidence for behavioural reciprocity and matching (per table 1). Whereas some strategies, reciprocity included, might work well in some ecologies, they are sub-optimal in others. One question for future research thus is how individuals learn to flexibly adapt their interaction strategies depending on specific socio-ecologies and the concomitant opportunities afforded by cooperation, alongside the need to protect against possible exploitation.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The simulated data and materials used in this study are available on Dryad [91].

Supplementary material is available online [92].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. A.R.: conceptualization, methodology, project administration, writing—original draft, writing—review and editing; A.S.S.: methodology, software, writing— review and editing; C.K.W.D.D.: conceptualization, methodology, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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