

Evolution of extortion in Iterated Prisoner's Dilemma games

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Iterated games are a fundamental component of economic and evolutionary game theory. They describe situations where two players interact repeatedly and have the ability to use conditional strategies that depend on the outcome of previous interactions, thus allowing for reciprocity. Recently, a new class of strategies has been proposed, so-called “zero-determinant” strategies. These strategies enforce a fixed linear relationship between one's own payoff and that of the other player. A subset of those strategies allows “extortioners” to ensure that any increase in one player's own payoff exceeds that of the other player by a fixed percentage. Here, we analyze the evolutionary performance of this new class of strategies. We show that in reasonably large populations, they can act as catalysts for the evolution of cooperation, similar to tit-for-tat, but that they are not the stable outcome of natural selection. In very small populations, however, extortioners hold their ground. Extortion strategies do particularly well in coevolutionary arms races between two distinct populations. Significantly, they benefit the population that evolves at the slower rate, an example of the so-called “Red King” effect. This may affect the evolution of interactions between host species and their endosymbionts.

replicator dynamics | adaptive dynamics

The Iterated Prisoner's Dilemma (IPD) has a long history as a model for the cultural and biological evolution of cooperation (1–9). A new class of so-called “zero-determinant” (ZD) strategies has recently attracted considerable attention (10–12). Such strategies allow players to enforce a linear relation unilaterally between one player's own payoff and the coplayer's payoff. A subset consists of the so-called “equalizer” strategies, which assign to the coplayer's score a predetermined value, independent of the coplayer's strategy (13). Another subset consists of the extortion strategies, which guarantee that one player's own surplus exceeds the coplayer's surplus by a fixed percentage. Press and Dyson (10) have explored the power of ZD strategies to manipulate any “evolutionary” opponent (i.e., any coplayer able to learn and to adapt).

In Stewart and Plotkin's (11) commentary to the article by Press and Dyson (10), they ask: “What does the existence of ZD strategies mean for evolutionary game theory: Can such strategies naturally arise by mutation, invade, and remain dominant in evolving populations?” In evolutionary game theory, it is the population that adapts: More and more players switch to the more successful strategies. From the outset, it may seem that the opportunities for extortion strategies are limited. If a strategy is successful, it will spread, and therefore be more likely to be matched against its like, but any two extortioners hold each other down to surplus zero. In a homogeneous population of extortioners, it is thus better to deviate by cooperating. Extortion is therefore evolutionarily unstable (12). However, we shall see that if the two players engaged in an IPD game belong to distinct populations, the evolutionary prospects of extortion improve significantly.

In the following, we investigate the impact of ZD strategies on evolutionary game theory. We show that in large, well-mixed populations, extortion strategies can play an important role, but only as catalysts for cooperation and not as a long-term outcome. However, if the IPD game is played between members of two

separate populations evolving on different time scales, extortion strategies can get the upper hand in whichever population evolves more slowly and enable it to enslave the other population, an interesting example of the so-called “Red King” effect (14).

The Prisoner's Dilemma (PD) game is a game between two players *I* and *II* having two strategies each, which we denote by *C* (“to cooperate”) and *D* (“to defect”). It is assumed that the payoff for two cooperating players, *R*, is larger than the payoff for two defecting players, *P*. If one player cooperates and the other defects, the defector's payoff *T* is larger than *R* and the cooperator's payoff *S* is smaller than *P*. Thus, the game is defined by $T > R > P > S$. An important special case is the so-called “donation game,” where each player can “cooperate” (play *C*) by providing a benefit *b* to the other player at his or her cost *c*, with $0 < c < b$. Then, $T = b$, $R = b - c$, $P = 0$, and $S = -c$.

In the IPD game, the two players are required to play an infinite number of rounds, and their payoffs P_I respectively (resp.) P_{II} are given by the limit in the mean of the payoffs per round. An important class of strategies consists of so-called “memory-one” strategies. They are given by the conditional probabilities p_R, p_S, p_T , and p_P to play *C* after experiencing outcome *R, S, T* resp. *P* in the previous round. [In addition, such a strategy has to specify the move in the first round, but this has only a transient effect and plays no role in the long run (15)]. An important class of memory-one strategies consists of reactive strategies, which only depend on the coplayer's move in the previous round (not one's own move). Then, $p_R = p_T =: p$ and $p_P = p_S =: q$, such that a reactive strategy corresponds to a point (p, q) in the unit square (16).

We will first define and characterize ZD strategies, equalizers, and extortioners. We then investigate, in the context of evolutionary game theory, the contest between extortioners and four of the most important memory-one strategies. We will show that extortion cannot be an outcome of evolution but can catalyze the emergence of cooperation. The same result will then be obtained if we consider all memory-one strategies. Hence, extortion strategies can only get a foothold if the population is very small. If the IPD game is played between members of two distinct populations, ZD strategies can emerge in the population that evolves more slowly. In particular, extortion strategies can allow host species to enslave their endosymbionts.

Methods and Results

Definitions. Press and Dyson (10) define the class of ZD strategies as those memory-one strategies (p_R, p_T, p_S, p_P) satisfying, for some real values α, β, γ , the equations

$$p_R - 1 = \alpha R + \beta R + \gamma \quad [1A]$$

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$$p_S - 1 = \alpha S + \beta T + \gamma \quad [1B]$$

$$p_T = \alpha T + \beta S + \gamma \quad [1C]$$

$$p_P = \alpha P + \beta P + \gamma. \quad [1D]$$

We note that $1 - p_R$ and $1 - p_S$ are the probabilities to switch from C to D , whereas p_T and p_P are the probabilities to switch from D to C . Press and Dyson (10) showed that if player I uses such a ZD strategy, then

$$\alpha P_I + \beta P_{II} + \gamma = 0, \quad [2]$$

no matter which strategy player II is using. Equalizer strategies are those ZD strategies for which $\alpha = 0 \neq \beta$, then

$$P_{II} = -\gamma / \beta. \quad [3]$$

Thus, player I can assign to the coplayer any payoff between P and R . (Indeed, because the p_i values have to be between 0 and 1, it follows that $\beta < 0$ and $P \leq P_{II} \leq R$). The so-called “ χ -extortion” strategies are those ZD strategies for which $\gamma = -(\alpha + \beta)P$, with $\chi := -\beta / \alpha > 1$. Then,

$$P_I - P = \chi(P_{II} - P).$$

In this case, player I can guarantee that his or her own “surplus” (over the maximin value P) is the χ -fold of the coplayer’s surplus. Fig. 1 shows examples of these different ZD strategies.

Press and Dyson (10) speak of ZD strategies because they use for their proof of Eq. 2 an ingenious method based on determinants. In Appendix A, we present a more elementary proof, following the method of Boerlijst et al. (13). Within the 4D unit cube of all memory-one strategies (p_R, p_S, p_T, p_P) , the ZD strategies form a 3D subset \mathcal{ZD} containing the 2D subsets \mathcal{EQ} and \mathcal{EX} of equalizers resp. extortioners (Appendix B). In Fig. 2, we sketch these sets for the reactive strategies.

Extortion Within One Population. To investigate the role of extortion in the context of evolutionary games, we concentrate on the donation game (in SI Text, we provide further results for the general IPD, which show that the main conclusions are independent of special characteristics of the donation game). We first consider how a χ -extortion strategy E_χ fares against some of the most important memory-one strategies, namely, tit for tat [$TFT = (1,0,1,0)$], always defect [$All D = (0,0,0,0)$], always cooperate [$All C = (1,1,1,1)$] and the win-stay-lose-shift strategy

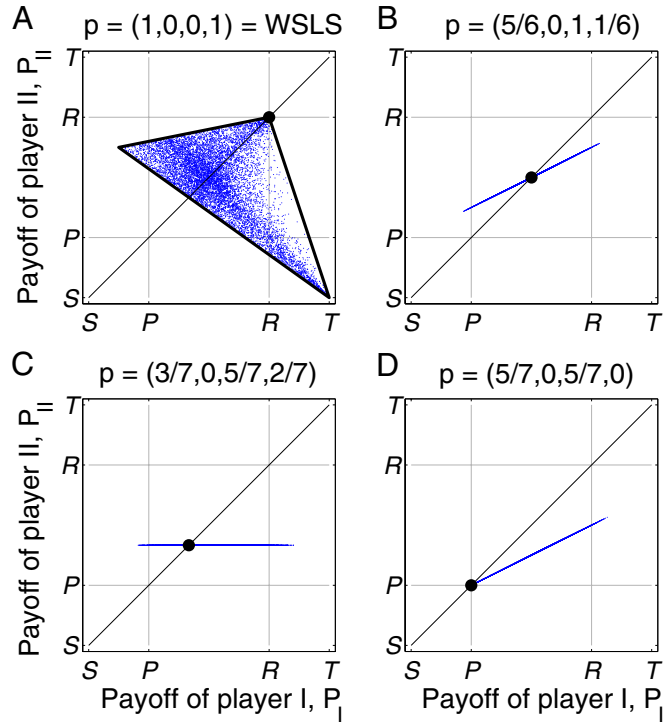


Fig. 1. Payoffs P_I and P_{II} of players I and II if both players use memory-one strategies in an IPD game (with $T = 3$, $R = 2$, $P = 0$, and $S = -1$). In each graph, the strategy of player I is fixed to some p , whereas the strategy q of the coplayer II can vary, sampling the 4D cube of memory-one strategies (the blue dots correspond to 10^4 different realizations of q). (A) In general, the payoff-pairs of the two players cover a 2D area, as here, when player I applies the strategy of WSLs (i.e., $p_R = p_P = 1$ and $p_S = p_T = 0$). (B) However, if player I adopts a ZD strategy, the possible payoff-pairs are restricted to a line. Two special classes of ZD strategies were highlighted by Press and Dyson (10): equalizers [strategies that set the coplayer’s score to a fixed value (the line of payoffs has slope zero)] (C), and extortioners [strategies that guarantee the surplus of player I is the χ -fold of the surplus of player II (i.e., $P_I - P = \chi(P_{II} - P)$, with $\chi > 1$ (the line of payoffs has a positive slope and intersects the diagonal at P)] (D).

WSLS, which is encoded by $(1, 0, 0, 1)$, and hence cooperates if and only if the coplayer’s move in the previous round was the same as one’s own move (7). We note that TFT is a ZD strategy and can be viewed as a limiting case of an extortion strategy, with $\chi = 1$. For the donation game, the payoff for a player using strategy i against a player using strategy j is given by the (i, j) th element of the following matrix:

	TFT	WSLS	E_χ	All C	All D
TFT	$(b - c) / 2$	$(b - c) / 2$	0	$b - c$	0
WSLS	$(b - c) / 2$	$b - c$	$\frac{b^2 - c^2}{b(1 + 2\chi) + c(2 + \chi)}$	$(2b - c) / 2$	$-c / 2$
E_χ	0	$\frac{(b^2 - c^2)\chi}{b(1 + 2\chi) + c(2 + \chi)}$	0	$\frac{(b^2 - c^2)\chi}{b\chi + c}$	0
All C	$b - c$	$(b - 2c) / 2$	$\frac{b^2 - c^2}{b\chi + c}$	$b - c$	$-c$
All D	0	$b / 2$	0	b	0

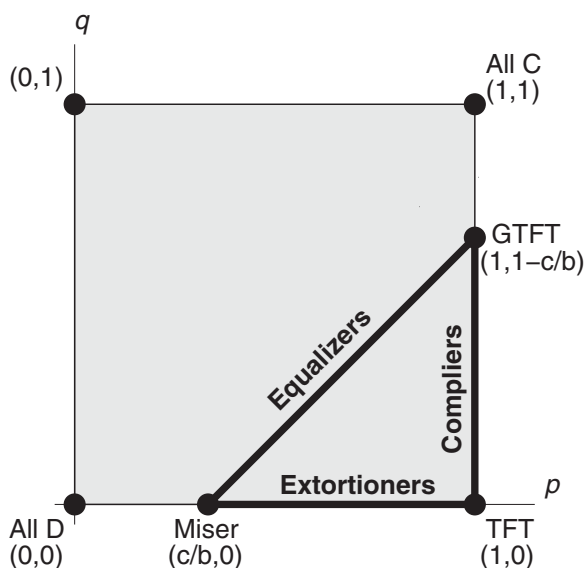


Fig. 2. Reactive strategies ($p_R = p_T = p$, $p_S = p_P = q$) for the donation game. All reactive strategies (the square $0 \leq p, q \leq 1$) are 2D strategies. The equalizer strategies are those on the segment between “generous TFT” (GTFT) ($p=1$, $q=1-c/b$) (16) and “Miser” ($p=c/b$, $q=0$) (30), the extortion strategies are those between Miser and TFT ($p=1$, $q=0$), and the “compliant” strategies (Discussion and ref. 11) are those between GTFT and TFT.

Let us start with the pairwise comparisons. The extortioner strategy E_χ is neutral with respect to *All D*. It is weakly dominated by *TFT*, in the sense that a *TFT* player does not fare better than an extortioner against extortioners but that interactions with other *TFT* players are giving an advantage to *TFT*. *All C* players can invade extortioners, and vice versa: These two strategies can stably coexist in proportions $c(\chi-1):(b+c)$. Finally, *WSLS* dominates extortioners (in the sense that *WSLS* provides a better response

than extortion against itself and against extortioners). We note that the mixed equilibrium of extortioners and unconditional cooperators can be invaded by each of the other three strategies. The same holds for the mixed equilibria of extortioners and unconditional defectors if the frequency of extortioners is sufficiently high. In particular, *TFT* can always invade such a mixed equilibrium but can, in turn, be invaded by *WSLS* or *All C*. No Nash equilibrium involves E_χ . If $b < 2c$, there are two Nash equilibria: a mixture of *TFT*, *All C*, and *All D*, and a mixture of *TFT*, *WSLS*, and *All D*. If $b > 2c$, there exist four Nash equilibria. In particular, *WSLS* is then a strict Nash equilibrium.

The replicator dynamics (17) displays for the payoff matrix continuous families of fixed points and periodic orbits, and hence is far from being structurally stable: Small changes in the dynamics can lead to vastly different outcomes. The same applies to most other deterministic game dynamics (18). It seems more reliable to consider a stochastic process that describes a finite, well-mixed population consisting of M players and evolving via copying of successful strategies and exploration (i.e., by a selection-mutation process) (19–21). Selection is viewed here as an imitation process; in each time step, two randomly chosen players A and B compare their average payoffs P_A and P_B , and A switches to B 's strategy with a probability given by $(1 + \exp[s(P_A - P_B)])^{-1}$, where $s \geq 0$ corresponds to “selection strength.” (As shown in *SI Text*, the details of the imitation process matter little.) Additionally, mutations occur with a small probability $\mu > 0$ (corresponding to the adoption of another strategy, with each alternative being equally likely). Any such stochastic process yields a steady-state distribution of strategies.

We find that although extortioners are never the most abundant strategy, they can play the role of a catalyzer. Indeed, if only *All D* and *WSLS* are available, a population may be trapped in a noncooperative state for a considerable time, leading to a mutation-selection equilibrium that clearly favors defectors (Fig. 3A). In such a case, extortioners (Fig. 3B) and *TFT* (Fig. 3C) offer an escape: These strategies can subvert an *All D* population through neutral drift and selection, respectively. Once defectors are rare, *WSLS* outperforms *TFT*, and it also prevails against extortioners if the population is sufficiently large (in a direct competition,

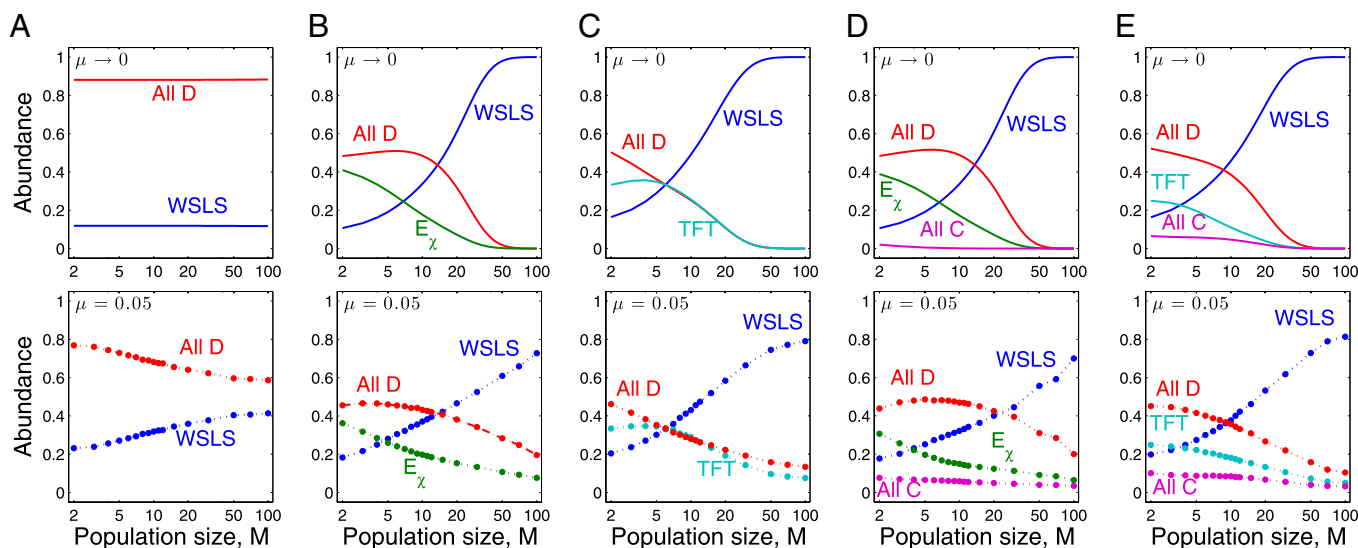


Fig. 3. Evolutionary competition between some important strategies in the IPD. For various population sizes M , the graphs show the frequency of each strategy in the mutation-selection equilibrium. We consider two mutation regimes: the limit of rare mutations $\mu \rightarrow 0$ (Upper), for which the equilibrium can be calculated analytically using the method of Fudenberg and Imhof (23), and a regime with mutation rate $\mu = 0.05$ (Lower), which is explored by individual-based simulations. For the copying process, we assume that individuals A and B are chosen randomly. A switches to B 's strategy with a probability given by $(1 + \exp[s(P_A - P_B)])^{-1}$, where P_A and P_B are the corresponding payoff values and $s \geq 0$ corresponds to “selection strength” (cf. ref. 21). (A) If *All D* competes with *WSLS*, the population is mostly in the defector's state, independent of population size and the mutation rate. (B and C) However, once E_χ or *TFT* is added, *WSLS* succeeds if populations are sufficiently large. *TFT* works slightly better than E_χ . (D and E) Adding *All C* only leads to minor changes in the stationary distribution, which now slightly favors E_χ . The parameters are $b=3$, $c=1$, $s=1$, and $\chi=2$.

WLS always gets a higher payoff than E_γ if $M > 1 + \chi$). Thus, in large populations, extortioners and *TFT* players tip the mutation-selection balance toward *WLS*, and therefore increase the level of cooperation. Further expansion of the strategy space through adding *All C* has only a small effect on the steady state (Fig. 3D and E), slightly favoring extortioners.

What happens when players are not restricted to the five specific strategies considered so far but can choose among all possible memory-one strategies? We study this by using the stochastic evolutionary dynamics of Imhof and Nowak (22), assuming that mutants can pick up any memory-one strategy, with a uniform probability distribution on the 4D unit cube. We further assume that the mutant reaches fixation, or is eliminated, before the next mutation occurs. Overall, this stochastic process leads to a sequence of monomorphic populations. The evolutionary importance of a given strategy can then be assessed by computing how often the state of the population is in its neighborhood. For a subset A of the set of memory-one strategies, we denote the δ -neighborhood of A (with respect to Euclidean distance) by A_δ , and let $\mu(A_\delta)$ denote the fraction of time that the evolving population visits A_δ . We say that A_δ is favored by selection if the evolutionary process visits A_δ more often than expected under neutral evolution, [i.e., if $\mu(A_\delta)$ is larger than the volume of the intersection of A_δ with the unit cube of all memory-one strategies]. We apply this concept to $A = \text{ZD}, \text{EQ}, \text{EX}$.

Extensive simulations indicate that neither extortioners nor equalizers or ZD strategies are favored by selection if the population is reasonably large (Fig. 4A). By contrast, very small population sizes promote the selection of these behaviors. For extortioners, this result is intuitive: In small populations, the fact that self-interactions are excluded yields greater weight to interactions with players using the rival strategy rather than interactions with players using one's own strategy (19); this effect may even result in the evolution of spite (24, 25). We address this point in more detail in *SI Text* (section 2). Essentially, both extortioners and equalizers suffer from not achieving maximal payoff $b - c$ against themselves, which causes their inherent instability, as also stressed by Adami and Hintze (12). The same holds for most ZD strategies. By contrast, *WLS* players do well against their like, and therefore prevail in the evolutionary dynamics for long periods if the population size is large, at least when $b > 2c$ or, for more general PD games, when $2R > T + P$ (15) (Fig. 4B). As a (possibly surprising) consequence, larger populations also yield higher

average payoffs (Fig. 4C). In *SI Text*, we show that these qualitative results are robust with respect to changes in parameter values, such as benefits and costs or the strength of selection. Hence, extortion is disfavored by evolution as soon as the population size exceeds a critical level.

Extortion Between Two Populations. Let us now consider two species (e.g., hosts and their symbionts) or two classes of a single species (e.g., old and young, buyers and sellers, rulers and subjects) engaged in an IPD game, which, of course, is now unlikely to be symmetrical. In such situations, extortioners may evolve even in large populations. Indeed, extortioners provide incentives to cooperate: As shown by Press and Dyson (10), *All C* is always a best response to an extortion strategy. In a single population of homogeneous players, this is not turned to advantage, because the extortioners' success leads to more interactions with their own kind. If extortioners evolve in one of two separate populations, they will not have to interact with coplayers of their own kind. Nevertheless, their success may be short-lived because they will be tempted to adopt the even more profitable *All D* strategy as a reaction to the *All C* coplayers who they have produced, which, in turns, leads to the disappearance of the *All C* players.

Extortioners can only achieve a lasting (rather than short-lived) success if the rate of adaptation for the host population is much slower than that for the symbionts. To elucidate this point, we extend our previous analysis by revisiting a coevolutionary model of Damore and Gore (26). These authors consider host-symbiont interactions where each host interacts with its own subpopulation of endosymbionts. Let us assume that these interactions are given by an IPD game. Members of both species reproduce with a probability proportional to their fitness (which is an increasing function of their payoffs) by replacing a randomly chosen organism of their species. However, the two populations of hosts and symbionts may evolve on different time scales, as measured by their relative evolutionary rate (RER). For an RER of 1, hosts and symbionts evolve at a similar pace in the evolutionary arms race and no population is able to extort the other (Fig. 5A). This changes drastically as soon as we increase the RER, by allowing symbionts to adapt more quickly. Fast adaptation results in a short-term increase of the symbionts' payoffs, because they can quickly adjust to their respective host. In the long term, however, this induces hosts to adopt extortion strategies (Fig. 5B), thereby forcing their symbionts to cooperate. Thus, it pays off in the long run for

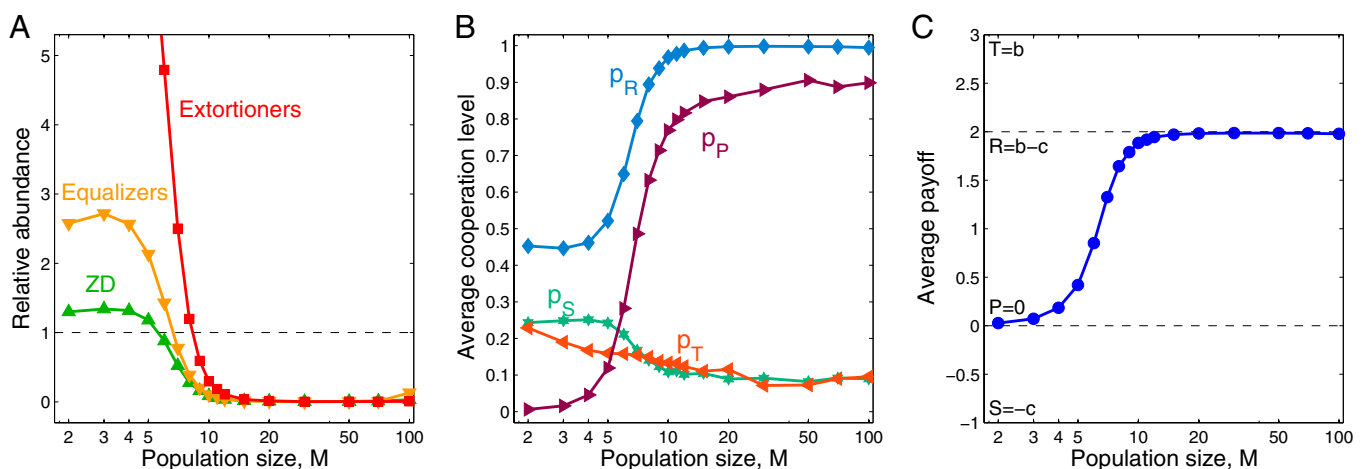


Fig. 4. Statistics of the evolutionary dynamics for memory-one strategies for a range of different population sizes. We have calculated the relative abundance of extortioners, equalizers, and ZD strategies (i.e., the time spent in a δ -neighborhood) divided by the volume of the intersection of that neighborhood with the set of memory-one strategies (A), the average strategy of the population (B), and the average payoff (C). Extortioners, equalizers, and ZD strategies are only favored for small population sizes. As the population size increases, individuals tend to apply *WLS*-like strategies and to cooperate only after mutual cooperation or mutual defection. As a result, the average payoff increases with population size. For the simulations, 10^7 mutant strategies were randomly drawn from the space of memory-one strategies. As in the study by Imhof and Nowak (22), the switch from a monomorphic population using strategy X to a monomorphic population using strategy Y occurred with the probability of fixation of a single Y mutant in a population of X residents. The parameters are $b = 3$, $c = 1$, $\delta = 0.1$, and $s = 100$.

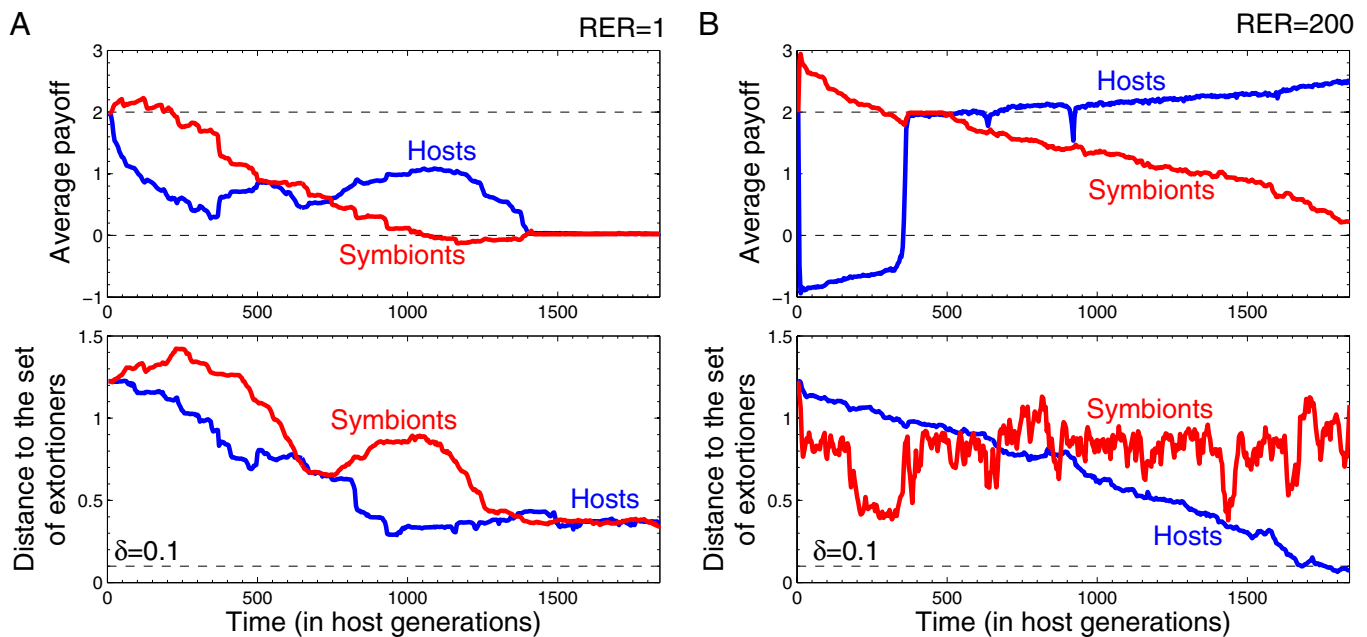


Fig. 5. Evolution of extortion in host-symbiont interactions. The graphs show two typical simulation runs for a population of 40 hosts, with each having a subpopulation of 20 symbionts. For each simulation run, one graph (*Upper*) shows the average payoff for each population, whereas the other graph (*Lower*) shows the Euclidean distance of each population to the set of extortioners (which can be 1.5275 at most). In the initial population, all individuals cooperate unconditionally. Further evolution depends on the RER. (*A*) If RER = 1, both species converge toward *All D* and no population is able to extort the other. (*B*) For RER = 200, symbionts evolve much more quickly. In the short term, they can thus increase their average payoff by switching to a noncooperative strategy. However, in the long term, hosts apply extortion strategies to force their symbionts to cooperate. Eventually, the hosts' payoff exceeds $b - c$, whereas the symbionts' payoff is close to zero. To model the evolutionary process, we followed the method of Damore and Gore (26). Whenever a symbiont reproduces, its offspring remains associated with the same host. Whenever the host reproduces, the new host offspring acquires its symbionts from other hosts (horizontal transmission). Mutations occur with probability $\mu = 0.05$, by adding Gaussian noise to an entry of the memory-one strategy of the parent ($\sigma = 0.05$). The process is run for 2,000 host generations (corresponding to more than 10^6 reproduction events for RER = 1 and more than 3×10^8 reproduction events for RER = 200). The other parameters are $b = 3$, $c = 1$, and $s = 10$.

the host to be slow to evolve; for the parameters in Fig. 5*B*, the resulting equilibrium allocates them, on average, a surplus more than 10-fold larger than the surplus achieved by the symbionts.

Discussion

Our main results show that within one population, extortion strategies can act as catalyzers for cooperation but prevail only if the population size is very small, and that in interactions between two populations, extortion can emerge if the rates of evolution differ. This holds not only for the donation game (and therefore whenever $R + P = T + S$) but in considerably more general contexts. In the last part of *SI Text*, we emphasize this robustness. We could also assume that the players alternate their moves in the donation game (27, 28) or that the underlying PD game is asymmetrical (the definitions have to be modified in a straightforward way). As noted by Press and Dyson (10), some results hold also for non-PD games; this deserves further investigation.

In orthodox game theory, strategy *A* dominates strategy *B* if *A* yields at least the payoff of *B* no matter what the coplayer does. When Press and Dyson (10) argue that extortioners dominate their coplayers, they mean that no matter what the coplayer does, the extortioner gets more. This is not quite the same, and we display in *SI Text* (section 2) an example that highlights the difference. Adami and Hintze (12) stress a similar point in their title: "Winning isn't everything." Moreover, when Press and Dyson (10) speak of evolutionary players, they refer to players who adapt their strategy in the course of an IPD game, whereas in evolutionary game theory, it is the population that evolves. Thus, Press and Dyson (10) analyzed ZD strategies in the context of classical game theory, with two players locked in contest: Extortion strategies play an important role in this context, as do the more orthodox trigger strategies (3, 6). In the context of evolutionary game theory, whole populations are engaged in the game. For a very small population size, extortion strategies still offer good prospects. This

is not surprising, because the limiting case, a population size $M = 2$, reduces to the scenario analyzed by Press and Dyson (10). In larger populations (with our parameter values for $M > 10$), the outcome is different. However, evolutionary game theory can reflect features of classical game theory if the two interacting players belong to two separate evolving populations.

Extortion strategies are only a small subset of ZD strategies. We have seen that within large populations, the class of ZD strategies is not favored by selection, in the sense that its neighborhood is not visited disproportionately often. This does not preclude, of course, that certain elements of the class are favored by selection. Thus, generous *TFT* ($1, 1 - c/b, 1, 1 - c/b$) does well, as do other less known strategies. In particular, Stewart and Plotkin (11) highlighted a class of strategies defined, instead of Eq. 3, by $P_I - R = \chi(P_{II} - R)$ (with $\chi > 1$). A player using this strategy does not claim a larger portion of the surplus but a larger share of the loss (relative to the outcome R of full cooperation). Remarkably, these "compliant" strategies do as well as *WSLS*. They are the only ZD strategies that are best replies against themselves.

In the study by Adami and Hintze (12), the evolutionary stability of several ZD strategies was tested by replicator dynamics and agent-based simulations, which independently confirm the result that these strategies do not prevail in large populations. They used a population size of $M = 1,024$, and payoff values of $R = 3$, $S = 0$, $T = 5$, and $P = 1$ (i.e., a PD game that cannot be reduced to a donation game). Adami and Hintze (12) also discuss the evolutionary success of "tag-based" strategies, which use extortion only against those opponents who do not share their tag. These strategies are not memory-one strategies because they depend not only on the previous move; rather, they use memory-one strategies in specific contexts, which depend on the tag. Such a tag is an additional trait that has to evolve and risks being faked.

In interactions between different populations, a cheater-proof tag is provided for free and extortion may accordingly evolve.

In endosymbiotic relationships, as we have seen, the species that evolves at the slower rate gains a disproportionate share of the benefit, an instance of the Red King effect (14, 29, 30). This requires two conditions to be met: Individuals need to come from different populations, and these populations have to evolve on different time scales. If these conditions are fulfilled, extortioner hosts can manipulate their symbionts' evolutionary landscape in such a way that the hosts' and the symbionts' payoffs are perfectly correlated. This ensures that only those symbiont mutants that are beneficial for the host can succeed. In this sense, such hosts apply an evolutionary kind of mechanism design; they create an environment that makes the symbionts' cooperation profitable for the symbionts but even more profitable for themselves.

Appendix A: Proof of Eq. 2

Let us denote by $P_I(n)$ and $P_{II}(n)$ the players' payoffs in round n ; by $s_i(n)$ the probability that I experiences outcome $i \in \{R, S, T, P\}$ in that round; and by $q_i(n)$ the conditional probability, given outcome i , that II plays C in round $n + 1$. By conditioning on round n , we see that $s_R(n + 1)$ is given by

$$s_R(n)q_R(n)p_R + s_S(n)q_S(n)p_S + s_T(n)q_T(n)p_T + s_P(n)q_P(n)p_P,$$

and $s_S(n + 1)$ is given by

$$s_R(n)(1 - q_R(n))p_R + s_S(n)(1 - q_S(n))p_S + s_T(n)(1 - q_T(n))p_T + s_P(n)(1 - q_P(n))p_P.$$

Hence, the probability that I plays C in round $n + 1$ [i.e., $p_C(n + 1) = s_R(n + 1) + s_S(n + 1)$], is given by $\mathbf{s}(n) \cdot \mathbf{p} = \mathbf{s}(n) \cdot [\alpha \mathbf{g}_I + \beta \mathbf{g}_{II} + \gamma \mathbf{1} + \mathbf{g}_0]$, where $\mathbf{g}_I := (R, S, T, P)$, $\mathbf{g}_{II} := (R, T, S, P)$, $\mathbf{1} = (1, 1, 1, 1)$, and $\mathbf{g}_0 = (1, 1, 0, 0)$. Thus, $w(n) := p_C(n + 1) - p_C(n)$ is given by

$$\alpha \mathbf{s}(n) \cdot \mathbf{g}_I + \beta \mathbf{s}(n) \cdot \mathbf{g}_{II} + \gamma \mathbf{s}(n) \cdot \mathbf{1},$$

which is just $\alpha P_I(n) + \beta P_{II}(n) + \gamma$. Summing $w(n)$ over $n = 0, 1, \dots, N - 1$ and dividing by N , we obtain

$$\frac{p_C(N) - p_C(0)}{N} \rightarrow \alpha P_I + \beta P_{II} + \gamma;$$

hence, Eq. 2 holds, independent of the strategy of player II . The same proof works for any 2×2 game (even if it is asymmetrical;

one just has to replace \mathbf{g}_{II} with the corresponding payoff vector). In many cases, however, there will be no solutions to Eq. 1 that are feasible (i.e., probabilities between 0 and 1).

Appendix B: Sets \mathcal{ZD} , \mathcal{EQ} , and \mathcal{EX}

Elementary algebra shows that within the 4D unit cube of all memory-one strategies (p_R, p_S, p_T, p_P) , the ZD strategies are characterized by

$$(1 - p_R)(S + T - 2P) + (1 - p_S)(P - R) + p_T(R - P) + p_P(S + T - 2R) = 0,$$

(a 3D subset of the cube). Equalizers are characterized, in addition, by

$$(R - P)(p_S - p_T - 1) = (T - S)(p_R - p_P - 1),$$

(they form a 2D set), and χ -extortion strategies are also characterized by $p_P = 0$ and

$$p_T[P - S + (T - P)\chi] = (1 - p_S)[T - P + (P - S)\chi]$$

(for each χ , a 1D set). In the special case of the donation game, these equations reduce to

$$p_R + p_P = p_S + p_T,$$

$$(b - c)(p_S - p_T - 1) = (b + c)(p_R - p_P - 1),$$

$$p_T(c + \chi b) = (1 - p_S)(b + \chi c),$$

respectively. The set \mathcal{EQ} of equalizers is spanned by $(1, 1, 0, 0)$, $(c/b, 0, c/b, 0)$, $(\frac{2c}{b+c}, 0, 1, \frac{b-c}{b+c})$, and $(1, 1 - c/b, 1, 1 - c/b)$, and the set \mathcal{EX} of extortion strategies is spanned by $(1, 1, 0, 0)$, $(c/b, 0, c/b, 0)$, and $(1, 0, 1, 0)$. All reactive strategies are ZD strategies, the reactive equalizers are those satisfying $p - q = c/b$, and the reactive χ -extortioners are those with $q = 0$ and $p = (b + \chi c) / (c + \chi b)$ (Fig. 2).

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Supporting Information

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SI Text

In the following, we provide additional information on the impact of extortioners and zero-determinant (ZD) strategies on the evolution in Iterated Prisoner's Dilemma (IPD) games. In section 1, we demonstrate how extortion strategies can help to promote cooperation when the population is trapped in a noncooperative state. In section 2, we discuss why small populations favor the evolution of extortion, whereas large populations give rise to win-stay-lose-shift strategy (*WLSL*)-like behavior. In section 3, finally, we provide further simulations to show that our qualitative results remain unchanged if the specific payoff values are changed, if the strength of selection is varied, or if a different evolutionary process is considered.

1. Extortioners as Catalysts for Cooperation

The win-stay, lose-shift strategy (*WLSL*) is an effective means to establish cooperation in a population (1–3). However, when competing with Always Defect (*All D*), the resulting payoff matrix for the donation game becomes

$$\begin{array}{c|cc} & \text{WLSL} & \text{AllD} \\ \hline \text{WLSL} & b-c & -c/2, \\ \text{AllD} & b/2 & 0 \end{array} \quad [\text{S1}]$$

indicating that for benefit $b > 2c$, where c is cost, the dynamics is bistable. If the initial fraction of *WLSL* players is below $\hat{x}_W = \frac{c}{b-c}$, their payoff is below average. In well-mixed infinite populations, replicator dynamics thus predicts that *WLSL* goes extinct. In finite populations, stochastic fluctuations may lift the fraction of *WLSL* players above the critical threshold \hat{x}_W . This, however, may take a substantial amount of time, during which the population is trapped in a noncooperative state with low payoffs (Fig. S1A). Moreover, if $\hat{x}_W > \frac{1}{2}$ (meaning that *All D* has the larger basin of attraction), *All D* has a larger share in the long-term mutation-selection equilibrium for all population sizes and for all mutation rates (as confirmed by Fig. 3A).

Adding extortioners to the game, the payoff matrix becomes

$$\begin{array}{c|ccc} & \text{WLSL} & \text{AllD} & E_\chi \\ \hline \text{WLSL} & b-c & -c/2 & \frac{b^2-c^2}{b(1+2\chi)+c(2+\chi)} \\ \text{AllD} & b/2 & 0 & 0 \\ E_\chi & \frac{(b^2-c^2)\chi}{b(1+2\chi)+c(2+\chi)} & 0 & 0 \end{array} \quad [\text{S2}]$$

This payoff matrix shows that when *WLSL* is rare, extortioners and defectors are almost indistinguishable. Thus, the fraction of extortioners may increase due to neutral drift (Fig. S1B). As soon as extortioners are common, *WLSL* can take over. Indeed, for any extortion factor $\chi > 1$, we have

$$\begin{aligned} b-c &> \frac{(b^2-c^2)\chi}{b(1+2\chi)+c(2+\chi)}, \\ \frac{b^2-c^2}{b(1+2\chi)+c(2+\chi)} &> 0 \end{aligned} \quad [\text{S3}]$$

This implies that although an extortioner outperforms a *WLSL* player in a direct pairwise competition, it is the *WLSL* player who

obtains the higher average payoff over the whole population. As a consequence, *WLSL* can invade, and once common, it is stable against invasion of the other two strategies, provided $b > 2c$. The resulting average payoff is close to the optimum $b-c$ (Fig. S1B). In sufficiently large populations, *WLSL* thus becomes the most abundant strategy in the mutation-selection equilibrium (as shown in Fig. 3B).

2. Effect of Population Size on the Evolution of Extortion and WLSL

Population size can have a considerable impact on the dynamics of evolutionary games in well-mixed populations (4–6). A major difference between small and large populations is due to the seemingly trivial fact that individuals cannot play against themselves. In large populations, this fact does not really matter; the payoff that players would get against themselves has a negligible influence on their average payoff. In small populations, however, the fact that self-interactions are excluded (and thus the payoff that one gets against players using the same strategy becomes relatively less important) can lead to drastic changes in the evolutionary dynamics.

To illustrate this impact of population size on the evolution of strategies in the IPD, let us consider the competition between *WLSL* and the extortioner strategy E_χ . For convenience, let us assume that the IPD takes the form of a donation game with parameters $b = 3$ and $c = 1$, and that the extortion factor is set to $\chi = 100$ (the general argument is independent of these specific parameter values, as we will show below). In this case, the rounded payoffs are

$$\begin{array}{c|cc} & \text{WLSL} & E_\chi \\ \hline \text{WLSL} & 2.00 & 0.01 \\ E_\chi & 1.13 & 0.00 \end{array} \quad [\text{S4}]$$

In this game, extortion is a dominated strategy, in the sense that irrespective of the coplayer's decision, *WLSL* yields a higher payoff than E_χ . One would therefore expect that *WLSL* spreads in the population, independent of the population's current composition. Indeed, in an infinite population with 40% *WLSL* players, the respective payoff (P) values are

$$\begin{aligned} P_{\text{WLSL}} &= 2.00 \cdot 0.4 + 0.01 \cdot 0.6 = 0.81 \\ P_{E_\chi} &= 1.13 \cdot 0.4 + 0.00 \cdot 0.6 = 0.45. \end{aligned} \quad [\text{S5}]$$

Thus, $P_{\text{WLSL}} > P_{E_\chi}$, as expected. However, considering the same game in a population of size $M = 5$ leads to a different conclusion. Again assuming that 40% of the players apply *WLSL* (i.e., two players use *WLSL* and three players use E_χ), the payoffs become

$$\begin{aligned} P_{\text{WLSL}} &= 2.00 \cdot \frac{1}{4} + 0.01 \cdot \frac{3}{4} = 0.51 \\ P_{E_\chi} &= 1.13 \cdot \frac{2}{4} + 0.00 \cdot \frac{2}{4} = 0.57. \end{aligned} \quad [\text{S6}]$$

In small populations, extortioners can therefore succeed against *WLSL*. A closer inspection of this example reveals that such a reversal of payoff relations occurs because extortioners beat *WLSL* players in a direct pairwise competition (as in the example above, where $1.13 > 0.01$). Because E_χ never loses any pairwise competition by its definition, this explains why extortioners are particularly strong in small populations [a more detailed discussion of

the impact of population size in a similar example is provided by Hilbe (6)].

As a consequence, extortioners can only act as catalysts for the cooperative *WSLS* strategy if the population size is above a critical threshold. This threshold is quite moderate. As shown in Fig. S2A, *WSLS*-like strategies are played by more than 98% of all residents if the population size exceeds $M = 20$ [which is in line with previous findings (1–3)]. Because *WSLS* is not close to the set of *ZD* strategies (the distance between *WSLS* and *ZD* is half the diameter of the cube of memory-one strategies), the strong performance of *WSLS* can be viewed as the major cause for the downfall of *ZD* strategies in large populations, whenever $b > 2c$ (as shown in Fig. 4). Two reasons for the strong performance of *WSLS* in large populations are that (i) evolutionary trajectories can lead to *WSLS* due to the catalytical effect of extortion and tit-for-tat (*TFT*)-like strategies, and (ii) *WSLS* is stable against invasion by other strategies.

Overall, these results indicate that the different outcomes in small and large populations are mainly due to the fact that self-interactions are impossible (and thus the payoff that one gets against others becomes more important). To illustrate this point further, we have run simulations where we allow for self-interactions (Figs. S3 and S4). When self-interactions are allowed, we observe that *WSLS*-like behaviors are also favored in small populations. *ZD* strategists, extortioners, and equalizers, on the other hand, become clearly negligible as the population size exceeds $M > 5$.

3. Robustness of the Results

Dependence on the Parameters. To test whether our results depend on the choice of parameters, we have run additional simulations for different benefit values b , and for varying selection strength s . As shown in Fig. S5, our qualitative results are robust for all parameter values considered: *ZD* strategies, extortioners, and equalizers are favored in small populations but disfavored in large populations. This trend is amplified when selection is strong, but it can also be observed for intermediate selection strengths.

Dependence on the Evolutionary Process Considered. The previous results for the evolution of extortion within one population were derived for evolutionary dynamics describing a pairwise imitation process. To test whether our results depend on that specific evolutionary process, we have rerun all simulations using a Wright–Fisher process instead (7). In contrast to the pairwise imitation model, the Wright–Fisher process assumes nonoverlapping generations. The probability that an individual in the next population applies strategy i is proportional to the number of i players in the previous generation and to the fitness of strategy i . For the fitness

of strategy i , we used an exponential specification, $f_i = \exp(s \cdot P_i)$, where, again, s denotes the strength of selection. As shown in Figs. S6 and S7, the qualitative results remain unchanged: (i) extortioners, equalizers, and *ZD* strategies are most abundant for small population sizes; (ii) in large populations, extortioners can promote the evolution of *WSLS*; and (iii) the average payoff increases with population size.

Dependence on the Payoff Structure. To explore the impact of the payoff values, particularly our choice of the donation game, we have repeated all computations for general IPD games. In Fig. S8, we show the outcome for the competition between the strategies *All D*, *WSLS*, E_χ , *TFT*, and Always Cooperate (*All C*), when the payoff parameters are set to the frequently used values $R = 3$, $P = 1$, and $S = 0$, where R is the payoff for cooperating players, P is the payoff for defecting players, and S is the sucker's payoff, and letting the temptation payoff T vary between 3 and 5. For $T = 4$, this yields “equal gains from switching,” as in the donation game (i.e., $S + T = R + P$), whereas for $T = 5$, we recover the payoff values used by Press and Dyson (8), Stewart and Plotkin (9), and Adami and Hintze (10).

If the population only consists of *WSLS* and *All D*, defectors are the most abundant strategy for $T > 4$ (when *All D* becomes risk-dominant; Fig. S8A). If extortioners or *TFT* is added to the population, *WSLS* remains the most abundant strategy for a wider range of temptation values T (Fig. S8B and C). This positive effect of extortioners and *TFT* persists when unconditional cooperators are added to the population, as in Fig. S8D and E. Note that in all scenarios, the abundance of *WSLS* decreases as the temptation approaches $T = 5$; for $T + P \geq 2R$, *WSLS* becomes evolutionarily unstable.

However, when we consider the stochastic dynamics of memory-one strategies, we observe results that resemble the outcome of the donation game, even if the temptation value is chosen to be $T = 5$ (Fig. S9). For large population sizes, we still observe that the evolving strategies typically only cooperate after mutual cooperation and mutual defection (Fig. S9B). However, in contrast to the donation game, the typical values of the conditional probability p_P are lower (in Fig. 4, large populations result in $p_P \approx 0.9$, whereas for Fig. S9, we obtain $p_P \approx 0.67$). This reduction of p_P reduces the risk of exploitation by *All D* and thus makes these *WSLS*-like strategies more stable against invasion of defectors. Overall, Fig. S9 therefore shares all the qualitative features of the corresponding Fig. 4: The influence of *ZD* strategies decreases with population size (although extortioners remain favored by selection for population sizes up to $M \approx 20$), and average payoffs increase with population size.

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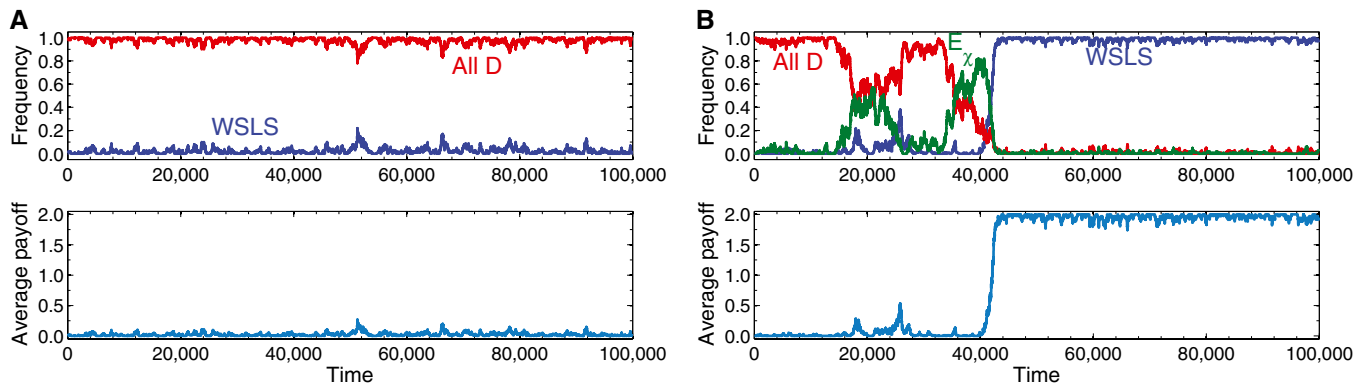


Fig. S1. Two typical simulation runs showing the catalyzing effect of extortion. (A) Between *All D* and *WLSL*, there is a bistable competition. This implies that if *WLSL* is rare in the initial population, it cannot invade. (B) If mutations can introduce extortioners, they can subvert *All D* by neutral drift. Once extortioners are common, *WLSL* can invade and take over the population. Parameter values are as follows: donation game with $b=3$ and $c=1$, extortion factor $\chi=2$, population size $M=100$, strength of selection $s=1$, and mutation rate $\mu=0.05$. E_χ , χ -extortion strategy.

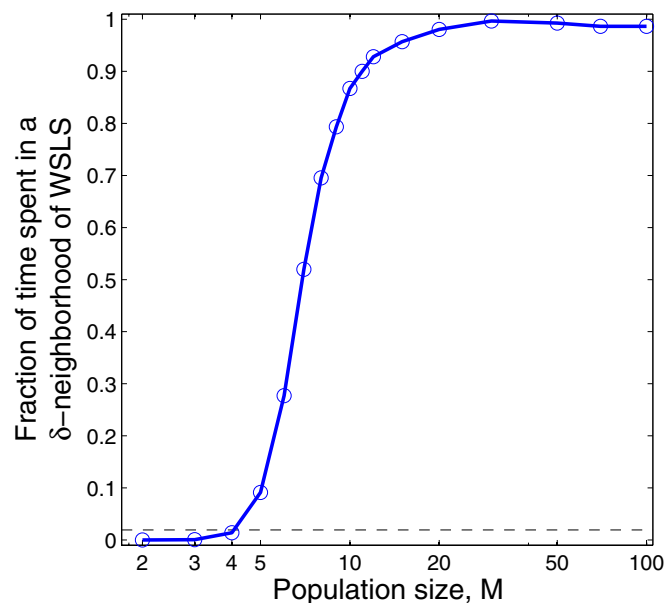


Fig. S2. Abundance of *WLSL*-like strategies for various population sizes (compare with Fig. 4). The graph shows how often the population applies a strategy that is δ -close to *WLSL* (for this graph, $\delta=0.5$ was used). If the population size exceeds $M=20$, *WLSL*-like strategies are played for more than 98% of the time, whereas the volume of the corresponding δ -neighborhood is $\pi^2/512 \approx 0.019$ (as indicated by the dashed black line). Note that the distance between *WLSL* and the set \mathcal{ZD} is equal to 1; the ZD strategy that is closest to *WLSL* is $p = (\frac{1}{2}, \frac{1}{2}, \frac{1}{2}, \frac{1}{2})$. Consequently, none of these *WLSL*-like strategies is δ -close to the set \mathcal{ZD} . The strong evolutionary performance of *WLSL*-like strategies thereby explains the downfall of ZD strategies for large population sizes.

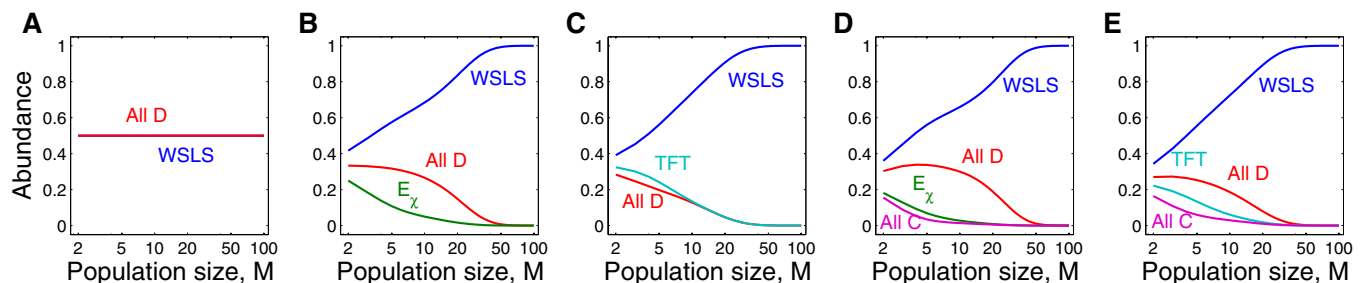


Fig. S3. Competition between the most important strategies when self-interactions are allowed. For these simulations, we consider the same scenario as in Fig. 3, but we assume that players are allowed to interact with themselves (which happens with probability $1/M$). Under this assumption, *WLSL* is the most abundant strategy across all population sizes if extortioners or *TFT* is present in the population (B–E). Only in a pairwise competition against defectors may *WLSL* be disfavored if *All D* has the larger basin of attraction; for the parameters considered here, the fixed point is at 1/2 and thus none of the strategies is risk-dominant (A). The parameters are $b=3$, $c=1$, and $s=1$ in the limit $\mu \rightarrow 0$. *All C*, Always Cooperate.

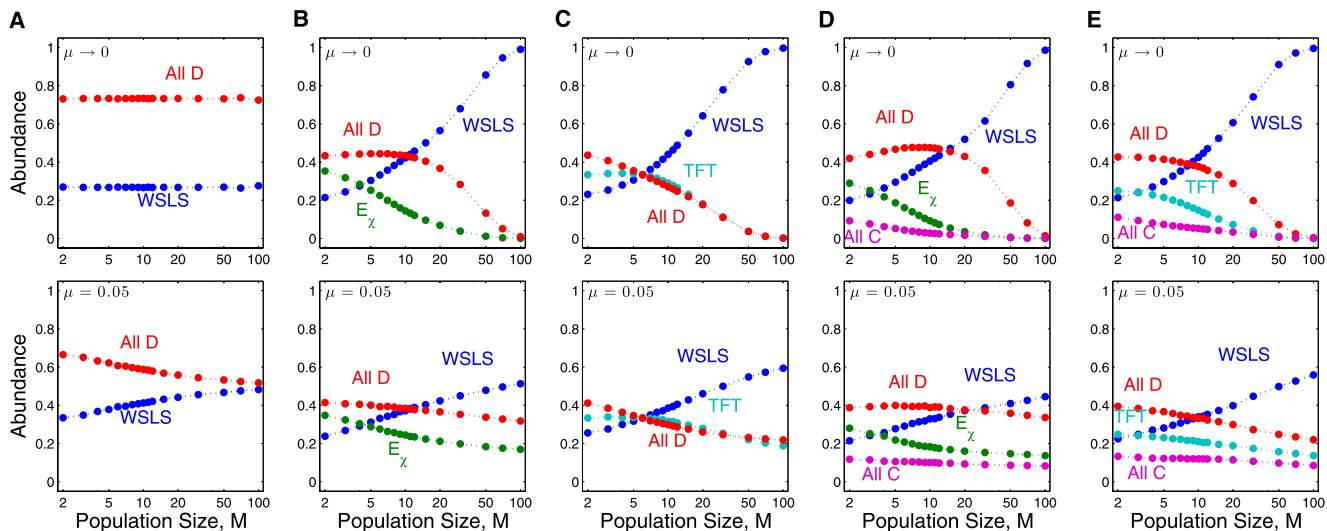


Fig. 56. Competition between some of the most important strategies for a Wright-Fisher process. All qualitative results agree with the pairwise imitation process (compare with Fig. 3): If *WLSL* competes with *All D*, defectors are favored by selection (**A**). However, extortioners and *TFT* can help *WLSL* to succeed in large populations (**B–C**). Unconditional cooperators have a negligible impact on the dynamics (**D–E**). Parameters: $b = 3$, $c = 1$, and $s = 0.25$. Simulations were run for 10^7 mutant strategies (*Upper*) and for 10^6 mutant strategies (*Lower*).

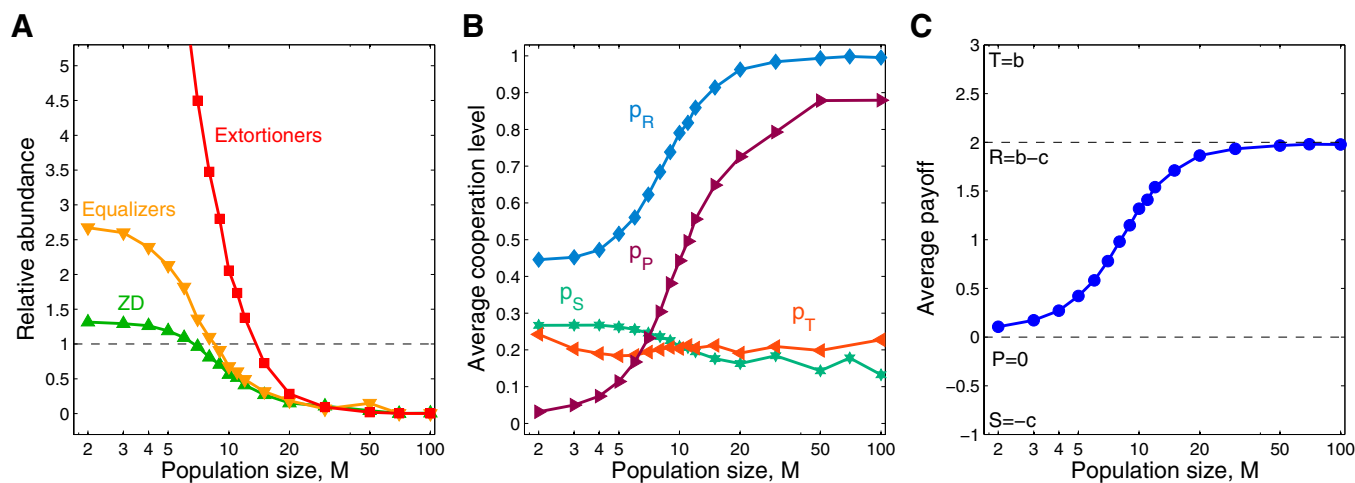


Fig. 57. Stochastic dynamics of memory-one strategies for a Wright-Fisher process. As in the pairwise imitation process, extortioners, equalizers and ZD strategies are disfavored by selection for large population sizes (**A**), for which *WLSL*-like behaviors take over (**B**). As a result, average payoffs increase in population size (**C**). Parameters are $b = 3$ and $c = 1$. Simulations were run for a sequence of 10^7 successive mutant strategies.

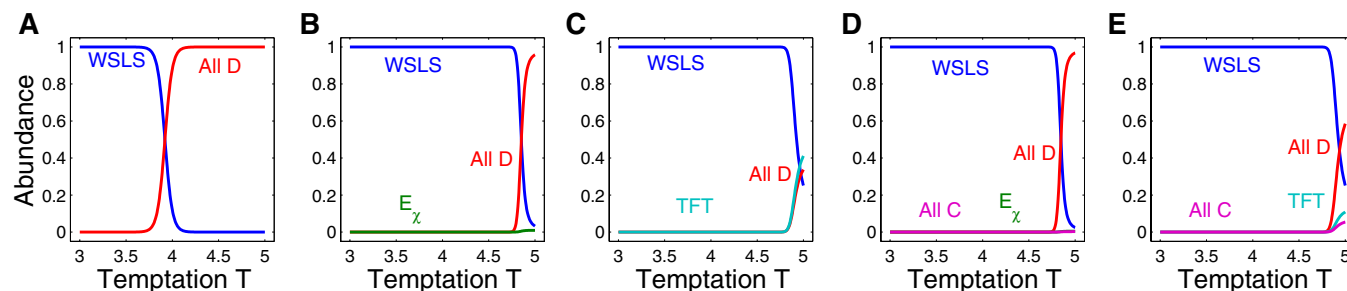


Fig. 58. Evolutionary competition between the most important strategies for the case of general IPD games. Each graph shows the adiabatic limit of rare mutations ($\mu \rightarrow 0$), where the payoff values were set to $S = 0$, $P = 1$, and $R = 3$, and T can vary between 3 and 5. In the absence of other strategies, *WLSL* is outperformed by *All D* if $T > 4$ (**A**). Adding extortioners or *TFT* helps *WLSL* to remain the most abundant strategy for a wider range of parameters (**B–E**).

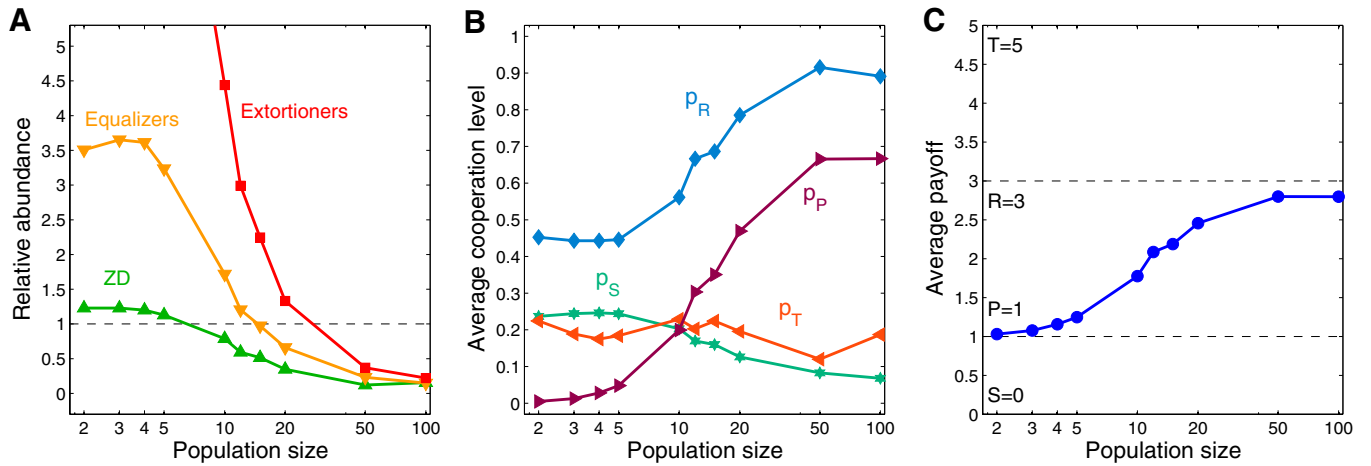


Fig. 59. Stochastic dynamics of memory-one strategies for the payoff values chosen by Press and Dyson (8), Stewart and Plotkin (9), and Adami and Hintze (10): $R=3$, $S=0$, $T=5$, and $P=1$. Interestingly, extortioners are favored by selection for a slightly wider range of population sizes than in the case of the donation game depicted in Fig. 4 (A). Nevertheless, as the population size increases, *WLSL*-like behaviors become more common (B), leading to a higher average payoff (C). Parameters are as in Fig. 4: $\delta=0.1$ and $s=100$. The process was run for 10^7 mutation events, starting from an initial population *All D*.