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**Manipulated into giving: when parasitism drives apparent
or incidental altruism**

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18 **Summary.** Altruistic acts involve the actor donating fitness to beneficiaries at net cost to
19 itself. In contrast, parasitic acts involve the actor extracting benefit from others at net cost to
20 the donors. Both behaviours may have the same direct net-cost transferral of fitness from
21 donor to beneficiary; the key difference between parasitism and altruism is thus who drives
22 the interaction. Identifying the evolutionary driver is not always straightforward in practice,
23 yet it is crucial in determining the conditions necessary to sustain such fitness exchange. Here
24 we put classical ecological competition into a novel game-theoretic framework in order to
25 distinguish altruism from parasitism. The distinction depends on the type of interaction that
26 beneficiaries have amongst themselves. When this is not costly, net-cost transferrals of fitness
27 from the donor are strongly altruistic, and sustained only by indirect benefits to the donor
28 from assortative mixing. When the interaction amongst beneficiaries is costly, however, net-
29 cost transferrals of fitness from the donor are sustainable without assortative mixing. The
30 donor is then forced into apparent or incidental altruism driven by parasitism from the
31 beneficiary. We consider various scenarios in which direct and indirect fitness consequences
32 of strong altruism may have different evolutionary drivers.

33 **Key words:** biofilms, cooperative trading, density dependence, hawk-dove game, prisoner's
34 dilemma, snowdrift game

35 **1. INTRODUCTION**

36 An act of altruism confers a fitness advantage on others, which is strong altruism if the actor
37 incurs a net fitness cost, and otherwise weak altruism [1,2]. The conferred advantage
38 expresses a transferral of fitness from altruist to beneficiary, although the magnitude of the
39 altruist's loss may differ from the magnitude of the beneficiary's gain. A parasitic act involves
40 a costly transferral of fitness by the donor to a beneficiary, just as in strong altruism, with the
41 crucial difference that the actor is the beneficiary and not the donor. The role of population

42 structure in sustaining these net-cost transferrals of fitness depends entirely on whether the
43 individual driving the interaction is the donor or the beneficiary. Strongly altruistic acts of
44 fitness transferral from donor to beneficiary can only be sustained by assorting mechanisms
45 that cause the benefits of altruism to be visited disproportionately on other altruists or its costs
46 to be cancelled by other indirect benefits [3-6]. In particular, assortative mixing that raises the
47 probability of interactions with kin reduces the temptation to defect from self-sacrificing or
48 other cooperative behaviours [1,7-9]. Parasitic acts of fitness transferral in contrast depend on
49 the relative efficiencies of parasite-attack and host-defence mechanisms, with no inherent
50 prerequisite for assorting mechanisms.

51 The initiator of an interaction, either as the donor in strong altruism or the beneficiary in
52 parasitism, is readily identified in many cases. For example, worker castes in societies of
53 eusocial insects clearly behave altruistically in renouncing their own reproductive potential
54 for the benefit of the colony [10]. An ant clearly does not act altruistically in hosting a
55 trematode fluke that will manipulate the ant's behaviour to its own benefit [11]. The identity
56 of the evolutionary driver is ambiguous in cases where the donor may gain indirectly from the
57 interaction with a beneficiary, as in reciprocal or kin-selected altruism, while the beneficiary's
58 direct gain is set against a direct cost of conflict with other beneficiaries, as in competition
59 amongst parasites for a limiting host resource. For example, a vampire bat may share its blood
60 meal with others at net cost to its own fitness in acts of strong altruism, which can be
61 sustained if the beneficiaries reciprocate or are kin [12]. Such indirect benefits do not exclude
62 the possibility that parasitic manipulation by competing beneficiaries drives selection for the
63 net-cost transferral of fitness, regardless of reciprocation or relatedness [13]. The behaviour is
64 then what we will term either 'apparent altruism', if it brings no indirect benefits to the donor,
65 or 'incidental altruism' if it brings indirect benefits which however have not motivated the
66 interaction. Empirical studies of populations with structured interactions may have little

67 evidence with which to distinguish these alternatives, and evolutionary theory lacks a
68 common framework for comparing the social interaction of altruism to the exploitative
69 interaction of parasitism.

70 Whether the donor or the beneficiary drives the net-cost transferral of fitness has major
71 consequences for understanding the proximal causes of the evolution of altruism, because a
72 donor-driven transferral is not stable without assortative mixing, whereas a beneficiary-driven
73 transferral is stable even in a freely mixed population. The objectives of this paper are to
74 demonstrate that (i) a two-strategy game-theoretic analysis can distinguish strong altruism
75 from parasitism only by reference to the absolute values of payoffs; (ii) the beneficiary may
76 drive selection for the net-cost transferral of fitness in parasitism, even if the donor drives
77 selection for the assortative mixing that sustains strong altruism.

78 We construct a formal game theoretic framework to set the evolution of cooperation in a
79 broader ecological context capable of distinguishing altruism from parasitism. Reformulation
80 of standard models from ecology within game theory shows that costly interactions amongst
81 beneficiaries make their interactions with the donor exploitative, and consequently sustainable
82 with or without assortative mixing of players. A net-cost transferral of fitness from donor to
83 beneficiary may be driven by parasitic manipulation, regardless of whether the donor achieves
84 indirect fitness gains from assortative mixing. This is an important clarification to current
85 understanding of strong altruism, which assumes that the evolution of its net-cost transferrals
86 of fitness is driven by the indirect fitness benefits to the donor resulting from assortative
87 mixing [1,3-7]. Competition amongst kin is then predicted to reduce selection for altruistic
88 behaviour [8,14-17]. Our game-theoretic framework for parasitism reveals how mutual
89 competition between parasitic beneficiaries can create selection for altruistic donors.

90 2. GAME-THEORETIC FRAMEWORK FOR TWO STRATEGIES

91 The problem of how traits for strong altruism can be favoured by natural selection is
92 embodied in a two-strategy game between two players. Each player is allowed to choose
93 between a strategy of social cooperation and a strategy of selfish defection. It then receives a
94 payoff that depends on its own and the other's strategy, as shown in table 1. Mutual
95 cooperation is not a stable strategy when its R ('Reward') payoff to each Cooperator is less
96 than the T ('Temptation') payoff to a Defector for unilateral defection. Moreover, unilateral
97 cooperation is not a winning strategy when its S ('Sucker') payoff to the Cooperator is less
98 than the P ('Penalty') payoff to each Defector for mutual defection. This is the Prisoner's
99 Dilemma (PD). Players of the PD find that unilateral defection against a Cooperator pays
100 better than mutual cooperation, and mutual defection pays better than unilateral cooperation.
101 The game is a social dilemma if the payoffs create a tension between individual welfare and
102 collective welfare given by the payoff sum for both players [18]. It is a useful analogy for
103 social evolution theory when the same-strategy payoffs R and P take the form of fitness
104 increments, and cross-strategy payoffs T and S can involve either a decrement or an increment
105 to fitness. For example, given a cooperative behaviour that confers fitness benefit b at net cost
106 c , a game may have payoffs $T = b$, $S = -c$, $R = b - c$, $P = 0$ [19,20]. The PD then represents the
107 problem that strong altruism, with $T > 0 > S$, is not a stable outcome amongst freely
108 interacting players. Any number of other relationships are possible between the fitness
109 payoffs T , S (or b , c) and R , P , depending on the scenario [20-26].

110 In order to bring exploitative interactions into game theory for two strategies, we
111 distinguish three different categories of games, according to whether the same-strategy
112 payoffs R and P are (i) both non-negative, or (ii) R is positive and P is negative, or (iii) both
113 are non-positive. All previous applications of two-strategy games to evolution have assumed a
114 non-negative Reward payoff. Whereas social evolution theory conventionally takes a non-

115 negative Penalty payoff [19-22], evolutionarily stable conflict can take positive Reward and
116 negative Penalty (e.g., in Hawk-Dove or Hawk-Mouse variants on Defector-Cooperator
117 games [23,24]. A zero Reward and negative Penalty can apply to games of selection for the
118 same trait ('kind selection') encompassing antigreenbeard traits [25,26]. Here we show that a
119 negative Reward and Penalty are appropriate to games involving competitive exploitation
120 amongst individuals. Our analysis of games across all three categories yields the complete set
121 of net-cost fitness transferrals from donor to beneficiary in altruistic and/or parasitic (or
122 predatory) interactions, regardless of how the magnitude of the donor's loss converts to the
123 beneficiary's gain.

124 We measure payoffs in the conventional way, as the change in fitness to the actor
125 resulting from the interaction with the recipient [2]. Payoffs are thereby calibrated against the
126 unavailable option of no interaction, corresponding to zero change [24]. We apply this
127 calibration to symmetric games, in which only four payoffs are possible from pairwise
128 interactions amongst two types of player. We enumerate all outcomes for these games at three
129 scales: (i) two strategies for two players ('strategic players'), (ii) two phenotypes in a single
130 population ('replicator dynamics'), and (iii) two genetically isolated populations ('ecological
131 dynamics').

132 **3. TWO-PLAYER DYNAMICS OF SOCIAL AND EXPLOITATIVE GAMES**

133 The Prisoner's Dilemma is one of four canonical games between a Cooperator and a Defector
134 that describe the complete 4-dimensional parameter space of payoffs. That is, each of these
135 games is defined by the relative values of T , R , S and P in the table-1 payoff matrix, from
136 which game theory determines the winning strategy (or equilibrium strategies). Figure 1(a)
137 shows thresholds of the payoff matrix for the four canonical games of Prisoner's Dilemma
138 (PD), Snow-Drift (SD, including evolutionarily stable Hawk-Dove or Hawk-Mouse games),
139 Harmony Game (HG), and Stag Hunt (SH). The coloured domains in figure 1(b) show the

140 game outcomes. The Prisoner's Dilemma is won by the Defector to the exclusion of the
141 Cooperator; the Snow-Drift game sustains both Defector and Cooperator (which may take the
142 roles respectively of Hawk and Dove/Mouse); the Harmony Game is won by the Cooperator
143 to the exclusion of the Defector; the Stag Hunt game has bi-stability [27].

144 Comparisons between games are facilitated by reducing the dimensionality, for example
145 by normalizing the rankings against a 1-unit Reward and zero Penalty [28,29]. In order to
146 facilitate the mapping of social with exploitation games, we introduce a more flexible
147 normalization that fixes the Reward at a constant R units and the Penalty at a lower value of P
148 $= \pm 1/R$. The condition $R > P$ encompasses three categories of games, illustrated in figures
149 2(a)-(c). These are: (a) a positive Penalty that is less beneficial than a positive Reward (shown
150 with $R > 1$, $P = 1/R$); (b) a negative Penalty and positive Reward ($P = -1/R$); (c) a Penalty that
151 is more costly than a negative Reward ($0 > R > -1$, $P = 1/R$). These alternatives preserve the
152 integrity of payoff rankings that define each game, such that the winning strategy remains
153 unchanged by the sign of the Reward and Penalty (e.g., cooperation never wins in the
154 Prisoner's Dilemma). For all three categories, their four games have unconfined domains,
155 extending indefinitely beyond the axes. Social dilemmas arise only below the angled pink
156 lines in figure 2, where collective welfare pays better than individual welfare ($2R > T + S$),
157 and the benefits of cooperation conflict with those of defection (greed prevails with $T > R$ or
158 fear prevails with $P > S$), always assuming $R > P$ [18]. The social dilemma ignores any
159 specifics about who initiates interactions, or their mechanisms or functions.

160 Assigning a positive value to R puts the origin of the Temptation-Sucker plane within the
161 SH domain when $P \geq 0$ (figure 2(a) for $P = 1/R$). The quartiles surrounding the origin
162 describe alternative payoffs for the Cooperator in terms of the four modes of social behaviour
163 in the Hamiltonian classification [2,30,31]: $+/+$ mutual benefit, $+/-$ strong altruism (stippled),
164 $-/-$ spite, or $-/+$ selfishness. The Cooperator in the mutual-benefit quartile is weakly altruistic

165 across the segment $T > S > 0$, defined by its altruistic transferral of fitness to the Defector ($T >$
166 S) combined with its net fitness gain ($S > 0$) distinguishing it from strong altruism. In contrast,
167 the Cooperator in the strong-altruism quartile is strongly altruistic throughout, defined by $T >$
168 $0 > S$, with the negative S expressing its net fitness loss relative to non-interaction. The
169 Cooperator strategy is not a stable outcome in the strong-altruism quartile. Selfishness is
170 stable in the Defector-only domain of PD, and mutual benefit is stable throughout the
171 coexistence domain of SD.

172 Given the possibility of games with a negative P , the origin of the Temptation-Sucker
173 plane is not constrained to the SH domain. In fact, the only domain from which it is excluded
174 is PD, because that would require $P > 0 > R$. Figure 2(b) shows the origin in HG for games
175 having same-strategy interactions that are beneficial for the Cooperator but costly for the
176 Defector ($R > 0 > P$). The immediate consequence of moving the origin out of SH is that the
177 +/- interaction is no longer confined to the Defector-only outcome of PD. It becomes an
178 alternative to the ++ interaction as a coexistence outcome within SD (stippled green sector),
179 and is sustained in the Cooperator-only HG (stippled blue sector).

180 Figure 2(c) shows the origin in the SD domain for games between two strategies that both
181 have negative same-strategy payoffs. The Cooperator strategy in this scenario may be
182 cooperative only in the relative sense of its same-strategy interaction (Cooperator-Cooperator)
183 being less costly than the Defector's same-strategy interaction (Defector-Defector). Now all
184 four types of interaction behaviour have coexistence outcomes in SD.

185 A Defector strategy with negative P gives coexistence outcomes the character of Hawk-
186 Dove or Hawk-Mouse conflicts [24]. The +/- interaction in the SD domains of figures 2(b)-
187 (c) more reasonably describe a manipulator-victim or parasite-host relationship than a selfish-
188 altruist relationship of the sort that applies to PD in figure 2(a), even for the social Cooperator
189 in figure 2(b).

190 For any social dilemma, and regardless of any normalization of same-strategy payoffs,
191 net-cost transferrals of fitness are excluded from SD only by $P \geq 0$. A net cost transferral of
192 fitness therefore has alternative domains set by P . It arises in PD amongst players with non-
193 negative P , where it is interpreted as strong altruism and cannot be sustained without
194 assortative mixing (e.g., kin selection). In the particular case of $P = 0$, and only in this case,
195 unilateral cooperation in PD is synonymous with strong altruism. Alternatively, the net-cost
196 transferral of fitness arises in SD amongst players that have negative P , where it is sustained
197 in freely mixing populations as victimization by an aggressor. Game theoretic treatments of
198 social evolution conventionally equate the cross-strategy interaction in PD with altruism
199 [5,19,32-36]. In order to demonstrate fully the danger of assuming this equivalence, we
200 further develop the analysis of games with negative P . The following two sections explain the
201 net-cost transferrals of fitness in SD in terms of replicator dynamics and ecological dynamics.

202 **4. WITHIN-POPULATION DYNAMICS OF SOCIAL AND EXPLOITATIVE GAMES**

203 Two-strategy games for two players are extended to two-strategy games for a population of
204 players for the purposes of modelling evolutionary change by frequency-dependent selection.
205 Here we use standard replicator dynamics to describe evolutionary games for a population of
206 two phenotypes, in which their relative frequencies in the population determine individual
207 fitness [37-39]. The equivalent ecological model then reveals the role of exploitative
208 interactions in sustaining net-cost transferrals of fitness between phenotypes.

209 Let strategies E_1 and E_2 have frequency-dependent expected payoffs $(\mathbf{A} \cdot \mathbf{x})_1$ and $(\mathbf{A} \cdot \mathbf{x})_2$ for
210 playing Cooperator and Defector respectively, where \mathbf{A} is the table-1 matrix of fitness
211 payoffs, and \mathbf{x} is the vector of fractions $x_1, 1 - x_1$ describing the relative frequencies of
212 Cooperator and Defector. The evolutionary success of strategy E_i is expressed as the
213 difference between its fitness and the average fitness: $(\mathbf{A} \cdot \mathbf{x})_i - \mathbf{x} \cdot \mathbf{A} \cdot \mathbf{x}$ [38]. For a large

214 population susceptible to continuously changing frequencies, this difference determines the
 215 per capita rate of change \dot{x}_i/x_i over time t . The replicator equation for each of two strategies
 216 is then

$$\dot{x}_i = x_i \cdot [(\mathbf{A} \cdot \mathbf{x})_i - \mathbf{x} \cdot \mathbf{A} \cdot \mathbf{x}]. \quad (4.1)$$

217 Solving for x_i in equation (4.1) at $\dot{x}_i = 0$ gives the evolutionarily stable frequency x_i^* of
 218 strategy E_i . This is 0 or 1 if $P \geq S$ and/or $R \geq T$, and otherwise takes positive stable fractions
 219 $x_1^* = (S - P)/(S - P + T - R)$ and $x_2^* = (T - R)/(S - P + T - R)$ [38]. These relative frequencies
 220 equal the probabilities of playing each strategy in the two-player game [24].

221 The two-phenotype replicator equation (4.1) is numerically equivalent to a single-
 222 genotype ecological model with the Lotka-Volterra form

$$\dot{y} = y \cdot [(S - P) + (R - T) \cdot y], \quad (4.2)$$

223 where $y = x_1/x_2$ and $x_2 \cdot t$ defines the time-scale [38]. A Cooperator strategy can invade the
 224 genotype on condition $S > P$, whereupon its ratio with a Defector strategy grows logistically
 225 on condition $T > R$, to equilibrium $y^* = (S - P)/(T - R)$.

226 Figures 2(a)-(c) model the categories of equilibrium outcome that apply equally to
 227 equations (4.1) and (4.2) on the T - S plane for positive and negative R and P , with $P = \pm 1/R$.
 228 Just as for two players, figures 2(b)-(c) show that a homogeneous population can sustain net-
 229 cost transferrals of fitness from Cooperator to Defector phenotype provided $P < 0$. The
 230 stippled green sector of the T - S plane sustains this type of interaction, and in a social dilemma
 231 below the angled pink line. The transferral of fitness from Cooperator to Defector is driven by
 232 the Defector sustainably exploiting the Cooperator in homogeneously mixed interactions, so
 233 without requirement for indirect fitness benefits to the Cooperator as in strong altruism.

234 An example illustrates the danger of assigning $P \geq 0$ to a scenario that may have costly
 235 same-strategy interactions. Meat sharing amongst non-kin chimpanzees has potential

236 explanations in reciprocal altruism or manipulative begging [40]. Consider a population
237 containing a Cooperator phenotype that donates meat to others at net cost to its own fitness,
238 and a Defector phenotype that benefits from the donated meat without reciprocating. The
239 meal-sharing process may be one of strong altruism by Cooperators or parasitic manipulation
240 by Defectors. Strong altruism is only sustainable if population structure or other mechanisms
241 of assortative mixing direct the benefits of altruism disproportionately to other altruists (or to
242 kin). In contrast, manipulation by Defectors has no structural pre-requisite given a negative
243 payoff for their same-strategy interactions ($P < 0$). Competition for mutually limiting
244 resources presents a natural interpretation for $P < 0$, when Defectors depress each other's
245 reproductive success below the intrinsic success achievable in the absence of others. Thus in
246 equation (4.2), $P < 0$ allows incursion into the Defector population by Cooperators that
247 themselves suffer competition with the Defectors ($S < 0$), always provided $S > P$. Under these
248 conditions, manipulative behaviour in an unstructured population once established may
249 subsequently favour selection on food donors to suffer it only from other donors (or kin). The
250 Cooperator phenotype then favours population structures that facilitate reciprocal (or kin-
251 selected) donation of fitness. The interaction is nevertheless incidental altruism driven by
252 parasitism for as long as $P < 0$ sustains the net-cost transferral of fitness even without such
253 population structures. Strong altruism cannot be the evolutionary driver of the +/- interaction
254 itself, it can only drive selection for the assortative mixing that confers indirect benefits on
255 donors through reciprocation (or kin beneficiaries). In effect, donors do not give benefit to
256 others in order to receive it back reciprocally or via kin, the benefit is taken from them by
257 others. To the extent that they are able, however, it makes sense for donors to limit the theft to
258 reciprocators or kin, for example by limiting dispersal (a form of 'social niche construction'
259 [41,42]). Similarly, intraspecific brood parasitism in birds can function as helping when the
260 host is a relative [43]. Any net fitness cost to an individual in hosting a relative's egg is

261 incidental altruism if the behaviour is sustained with no lower threshold for the indirect
 262 benefit to the host through relatedness.

263 5. BETWEEN-POPULATION DYNAMICS OF EXPLOITATIVE GAMES

264 The 1-dimensional system of equation (4.2) for a single population readily expands to
 265 accommodate two genetically isolated populations competing within and between their
 266 genotypes to exploit limiting resources. Standard Lotka-Volterra coupled rate equations
 267 describe the 2-dimensional population dynamics for a closed community:

$$\dot{n}_i = r_i \cdot n_i \cdot \left[1 + (\alpha_{ij} \cdot n_j - n_i) / k_i \right]. \quad (5.1)$$

268 For each Genotype-*i*, rate \dot{n}_i describes continuous change over time in abundance n_i , where k_i
 269 is its carrying capacity in the absence of the other genotype. Population change is determined
 270 by the intrinsic rate of increase per capita r_i , moderated by the density of both populations,
 271 with interaction coefficient α_{ij} measuring the impact on Genotype-*i* from Genotype-*j* relative
 272 to the normalized impact $\alpha_{ii} = -1$ on Genotype-*i* from its own type. For example, Genotype-*i*
 273 takes $\alpha_{ij} < 0$ if its population growth is impeded by competition from Genotype-*j*. The
 274 negative payoff to Genotype-*i* from the interaction then counts as a cost relative to intrinsic
 275 fitness r_i before any interactions.

276 In terms of a game, payoffs are measured relative to fitness r_i available prior to playing
 277 the game. The calibration of payoffs is manifested explicitly by viewing a Lotka-Volterra
 278 model for G genotypes as an equivalent replicator model for $G + 1$ phenotypes [38].

279 Accordingly, the equation-(5.1) model for genotypes $i = 1, 2$ translates to replicator equation

280 $\dot{x}_i = x_i \cdot \left[(\mathbf{A} \cdot \mathbf{x})_i - \mathbf{x} \cdot \mathbf{A} \cdot \mathbf{x} \right]$ for phenotypes $i = 1$ to 3 with $x_1 + x_2 + x_3 = 1$, taking payoff matrix

281 **A:**

$$\mathbf{A} = \begin{bmatrix} -k_2/k_1 & \alpha_{12} \cdot r_1/r_2 & r_1 \\ \alpha_{21} \cdot r_2/r_1 & -k_1/k_2 & r_2 \\ 0 & 0 & 0 \end{bmatrix}. \quad (5.2)$$

282 The bottom row of \mathbf{A} takes zeros, reflecting the absence of a third active strategy. \mathbf{A}_{13} and \mathbf{A}_{23}
 283 are then payoffs to Cooperator and Defector respectively without interactions.

284 Solving for n_i in equation (5.1) at $\dot{n}_i = 0$ gives its stable equilibrium population size:

$$n_i^* = k_i + \alpha_{ij} \cdot n_j, \quad (5.3)$$

285 Given $n_j^* = k_j$ when $n_i^* = 0$, solving for α_{ij} in equation (5.3) yields the necessary and
 286 sufficient condition for positive equilibrium abundance of Genotype- i (i.e., $n_i^* > 0$):

$$\alpha_{ij} > -k_i/k_j. \quad (5.4)$$

287 When both populations meet condition (5.4), equation (5.3) yields stable n_i at system
 288 equilibrium:

$$n_i^* = (k_i + \alpha_{ij} \cdot k_j) / (1 - \alpha_{ij} \cdot \alpha_{ji}). \quad (5.5)$$

289 These predictions describe the equilibrium outcomes of ecological processes defined by
 290 equation (5.1) for a two-strategy game played by two populations. They have been thoroughly
 291 analysed in ecological theory [44-46], though not at all in game theory.

292 Figure 2(d) shows how the α plane of interaction coefficients partitions into domains of
 293 equilibrium persistence for one or both genotypes on condition (5.4). The green domain
 294 encompasses stable equilibrium coexistence, with the populations growing monotonically, or
 295 in damped oscillations, to positive n_1^* and n_2^* . The white domain encompasses bi-stability.
 296 All four outcomes on the α plane have exactly corresponding outcomes on the Temptation-
 297 Sucker plane of figure 2(c), with assignment of cross-strategy payoffs $S = \alpha_{12}$ and $T = \alpha_{21}$. The
 298 mutual payoffs $R = -k_2/k_1$ and $P = -k_1/k_2$ enumerate the greater efficiency of G1 relative to G2
 299 in costly resource exploitation. They are forcibly non-positive because the carrying capacities
 300 k_1 and k_2 take non-negative values. With the Cooperator genotype G1 having the greater

301 carrying capacity, figure 2(d) has $-k_2/k_1 > -k_1/k_2$ just as figure 2(c) has $R > 1/R$ for $0 > R > -1$
302 and $P = 1/R$.

303 The α -plane origin must lie within the coexistence domain, given negative R . Figure 2(d)
304 shows its surrounding quartiles, which determine the identities of freely interacting
305 genotypes. The four alternatives are $+/+$ mutualistic, $+/-$ parasite-host, $-/-$ competitors, and
306 $-/+$ host-parasite [47]. Given the costly nature of same-genotype interactions, all cross-
307 genotype interactions involve forms of selfish exploitation, whether to mutual benefit or cost,
308 or to the benefit of one at the cost of the other. Within the domain of coexistence, positive or
309 negative α_{ij} for Genotype- i are expressed in larger or smaller n_i^* relative to k_i , as determined
310 by equation (5.5). Thus a genotype has parasitic status if it achieves higher equilibrium
311 abundance in the presence of the other genotype than on its own, resulting from a transferral
312 of fitness at net-cost to the other, which therefore has host status. For example, the dynamic of
313 cuckoos parasitizing the nests of other bird species is sustained in the model by the surrogate
314 parent genotype G1 having a sufficiently higher carrying capacity ($k_1 > k_2$) to compensate for
315 its net cost in fitness ($\alpha_{12} < 0$) from provisioning nestlings to the net benefit of the cuckoo
316 chick ($\alpha_{21} > 0$) with genotype G2. As a two-strategy game, the net-cost transferral of fitness
317 from the surrogate parent to the net benefit of the cuckoo chick ($T > 0 > S$) is sustained by
318 virtue of a sufficiently negative P to accommodate $0 > S > P$ in the SD domain. Whilst
319 cuckoos are unmistakably parasitic, net-cost transferrals of fitness between symbiotic species
320 can be sustained as altruism when indirect benefits accrue to relatives of the donor [48]. In
321 such cases, a game-theoretic analysis of the sort illustrated in figure 2(d) can identify apparent
322 or incidental altruism in which it is parasitism that drives the direct fitness benefits.

323 In game-theoretic terms, the population dynamics of two resource-limited genotypes can
324 only encompass all four games when the origin of the T - S plane is in the coexistence domain
325 of SD (figures 2(c)-(d)). To locate the origin in SH or HG (as figures 2(a)-(b)) would mean

326 that inter-genotype interactions are necessary to the persistence of one or both genotypes,
327 which in turn would rule out the existence of SH and HG and/or PD games. For example, a
328 predator G2 that depends on a prey G1 has standard Lotka-Volterra dynamics:

$$\dot{n}_1 = c_1 [1 - n_1 + \alpha_{12} \cdot n_2] \cdot n_1 - d_1 \cdot n_1, \quad \dot{n}_2 = c_2 \cdot \alpha_{21} \cdot n_1 \cdot n_2 - d_2 \cdot n_2. \quad (5.6)$$

329 The impacts of predation are measured in a fitness cost $\alpha_{12} < 0$ to each individual of the prey
330 population n_1 , and a corresponding fitness benefit $\alpha_{21} > 0$ to each individual of the predator
331 population n_2 . The α -plane origin lies in the G1-only domain (equivalent to the T - S plane
332 having its origin in HG), as a result of predator persistence requiring that α_{21} exceeds a
333 positive threshold R (specifically, $n^* = 0$ at $R = d_2/(c_2 \cdot k_1)$ where $k_1 = 1 - d_1/c_1$). Since G2
334 cannot persist without G1, the α plane has no domains equivalent to the game-theoretic PD
335 and SH (in effect, $P \rightarrow -\infty$).

336 **6. WHEN IS A NET-COST FITNESS TRANSFERRAL NOT STRONG ALTRUISM?**

337 The game-theoretic homology between victim or host responses to manipulation and strongly
338 altruistic acts is not a trivial issue of re-labelling an altruist as victim. It speaks directly to
339 questions about the evolutionary origins of cooperation, in ways that social game theory
340 cannot when it confines itself to games with $P \geq 0$, and therefore to already cooperative
341 players. For example, a strain of bacterium G1 that manufactures a public good in the form of
342 an extra-cellular polymeric biofilm may suffer its exploitation by a strain G2 that contributes
343 nothing to the public good [49]. These types of interactions are commonly construed as forms
344 of strong altruism requiring explanation in terms of population structure [25,50-51]. However,
345 equations (5.1)-(5.5) predict stable coexistence of the two strains as +/- parasite-host in
346 freely-mixing populations, provided G1 sufficiently compensates for its competitive
347 inferiority with superior carrying capacity. A detailed physiological model of the growth in
348 thickness of biofilms has predicted a potential competitive advantage to biofilm production in

349 sustaining access to oxygen, analogous to vertical growth in plants towards light [52]. Surface
350 layers of biofilm suffocate deeper layers, in interactions between strains consistent with
351 sustainable $-/-$ competition or $+/-$ parasitism in SD (figures 2(c)-(d)). Other acts of apparent
352 altruism may also have testable alternative explanations in terms of exploitation. For example,
353 plants that evolve to refrain from overshadowing their neighbours can be altruists [53]. An
354 alternative driver in competitive exclusion should not be ruled out, however, unless the same-
355 strategy interaction amongst beneficiaries has a non-negative fitness payoff.

356 Table 2 enumerates the full set of seven different social dilemmas and one HG that have
357 cross-strategy interactions with a net-cost payoff to Cooperators and net-benefit payoff to
358 Defectors. These include all combinations of game (PD, SD, HG, SH) with positive or
359 negative R and P and $+/-$ interactions between strategies, as stippled in figure 2. The three
360 occurrences of outcomes in PD, and the two in SD, emphasize that the cross-strategy
361 interactions in PD and SD are not synonymous with strong altruism and mutual benefit
362 respectively, except in the restrictive case of $P = 0$. The many alternative outcomes of $+/-$
363 interactions show that to assume non-negative same-strategy interactions ($R > P \geq 0$), if
364 inappropriate for the scenario at hand, will result in a host response to manipulation or
365 parasitism in SD being mistaken for strong altruism in PD.

366 Distinguishing between beneficial and costly same-strategy interactions requires
367 measuring the fitness increment or decrement due to R or P above or below the intrinsic
368 fitness available without interaction. For some eusocial insects or vertebrate societies in which
369 lone individuals have low or zero survival, same-strategy interactions clearly bring benefits.
370 In other cases, and particularly amongst microorganisms, it is not trivial to know whether
371 same-strategy interactions are beneficial or costly relative to no interaction, because the
372 reproductive success measurable in natural environments is usually that achieved in the
373 presence of intra- and inter-specific interactions. To assume a non-negative P , however, can

374 lead to multiple misconceptions. These include wrongly identifying or predicting altruism, or
375 wrongly interpreting the evolutionary driver of the net-cost transferral of fitness as kin-
376 selected or reciprocal altruism.

377 **7. DISCUSSION**

378 The mapping of replicator and Lotka-Volterra dynamics onto a common plane of payoffs for
379 cross-strategy interactions has defined the conceptual difference between altruistic and
380 parasitic interactions. We have shown how negative R and/or P are naturally conceived in
381 ecological scenarios of a two-phenotype population and of independently self-replicating
382 populations. They provide evolutionary game theory with an ecological framework for setting
383 net-cost transferrals of fitness within the SD domain of stable coexistence. Moreover, they
384 open ecological theory to game-theoretic analysis.

385 Conventional game theory for social evolution assigns non-negative payoffs to same-
386 strategy interactions, which are then consistent with the convention to consider social
387 behaviours as any interactions amongst same or cross strategies that have fitness
388 consequences for actor and recipient [2]. In order to include competitive interactions within
389 two-strategy games, we find it useful to consider a strategy as ‘social’ only if its same-
390 strategy interaction has a non-negative payoff, making it at least as good as no interaction.
391 The alternative to a social strategy is then an ‘unsocial’ strategy defined by a costly same-
392 strategy interaction, making it an adverse encounter typical of mutual competition for limiting
393 resource. Two-strategy games for two or more players assume that the game gets played,
394 whether the players have elected or been forced to play it. Given the distinction between
395 social and unsocial strategies, it makes sense to interpret a game as elected if both strategies
396 are social. Then neither strategy incurs a cost by playing its own type, even if one or both may
397 be susceptible to invasion by the other. Alternatively, a game is enforced if at least mutual
398 defection has a negative payoff. Then at least the strategy of mutual defection incurs a cost by

399 playing, as for example the impact of same-strategy competition on the intrinsic fitness prior
400 to density effects. Enforcement is thus by an extrinsic process, such as competition for
401 limiting resource.

402 It has long been recognized that competition within population structures can reduce or
403 cancel the net selective advantage of altruistic behaviour [8,14-17]. For kin structures, this
404 balancing of effects depends on competition being coupled to relatedness [8, 15,54,55]. Our
405 analysis is consistent with these results insofar as the strong altruism enacted by a Cooperator
406 in a PD game requires a larger sacrifice in the presence of the costly same-strategy
407 interactions typical of density-regulated competition (i.e., a more negative S in the PD
408 domains of figures 2(b)-(d) than in figure 2(a)). The PD prediction of a Defector-only
409 outcome applies to the case of homogenous competition and relatedness, and it is only the
410 decoupling of relatedness from competition that can allow the Cooperator to direct altruism at
411 kin. Crucially, however, the game theoretic representation of competition has shown how a
412 victim of parasitic manipulation also functions as an incidental altruist if it allows itself to be
413 victimized only by kin, in which case competition may motivate altruism via parasitic
414 manipulation. This is a distinct mechanism from the policing of altruism by coercion, which is
415 driven by altruists to enforce altruistic behaviours [4,56].

416 In the literature on the evolution of cooperation, the conventional application of game
417 theory is to discrete phenotypes with replicator dynamics in elected games. Ecological
418 contexts have involved building spatial structure into these dynamics. The addition of a third
419 dynamic variable of empty space to the replicator equation causes its two-phenotype
420 population to have lower density when Defectors predominate, which then favours the
421 production of Cooperators in randomly forming discrete interaction groups [3,57]. Higher
422 population densities resulting from the benefits of elected cooperation can promote spatial
423 heterogeneity in the distribution of Cooperators when Defectors diffuse slowly [58,59]. All of

424 these models use a positive Reward. They consequently obtain Cooperator and Defector
425 polymorphisms only with weak altruism in SD, or they depend on positive assortment of
426 strategies to sustain net-cost fitness transferrals between social players in PD [20].
427 Investigations of social dilemmas stand to benefit from the application of game theory to
428 competitive scenarios with negative R and/or negative P .

429 **8. CONCLUSIONS**

430 A net-cost transferral of fitness from strong altruist to beneficiary can be sustained without
431 assortative mixing; the only component of altruism that requires assortative mixing is the
432 indirect fitness gain that comes back to the donor as a result of its costly donation to kin or
433 other altruists. This distinction leads to recognition of a new range of states that we call
434 incidental altruism, in which parasitic exploitation by the beneficiary drives the direct fitness
435 cost to the donor while selection on the donor for assortative mixing drives its indirect fitness
436 gain from reciprocation or kin. Game-theoretic analyses have not previously considered this
437 route to the evolution of cooperative behaviour, which is potentially widespread under
438 density-dependent population regulation and has no lower threshold for assortative mixing. It
439 further suggests the possibility that empirical studies interpreting net-cost transferrals of
440 fitness as evidence of altruism may actually be seeing an interaction driven by parasitism
441 (which we call ‘apparent altruism’, unless accompanied by assortative mixing as ‘incidental
442 altruism’). Disaggregating the drivers for direct and indirect fitness consequences requires
443 knowledge of the absolute payoff for the interactions amongst the donor’s beneficiaries. Only
444 if this is non-negative is the net-cost transferral of fitness driven by altruism from the donor.

445

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569 Table 1. Matrix of interaction payoffs for the actor in two-strategy games, assuming $R > P$.

570

actor \ recipient	Cooperator	Defector
Cooperator	Reward, R	Sucker, S
Defector	Temptation, T	Penalty, P

571

572 Table 2. Specifications for the seven social dilemmas and one HG with net-cost transferrals of
 573 fitness from *C* Cooperators to *D* Defectors (the +/- interactions $T > 0 > S$, as stippled in figure
 574 2).

575

specification*	game	outcome	players	phenotypes	populations
(a) strong altruist to selfish beneficiary ($R > P \geq 0$)					
1. $T > R > P \geq 0 > S$	PD	<i>D</i> only	figure 2(a)	eqns (4.1), (4.2)	-
2. $R \geq T > 0, P \geq 0 > S$	SH	<i>C</i> or <i>D</i>	figure 2(a)	eqns (4.1), (4.2)	-
(b) apparent or incidental altruist victim to parasitic manipulation ($R \geq 0 > P$)					
3. $T > R \geq 0 > P \geq S$	PD	<i>D</i> only	figure 2(b)	eqns (4.1), (4.2)	-
4. $T > R \geq 0 > S > P$	SD	<i>C</i> and <i>D</i>	figure 2(b)	eqns (4.1), (4.2)	eqn (5.6)
5. $R \geq T \geq 0 > S > P$	HG	<i>C</i> only	figure 2(b)	eqns (4.1), (4.2)	eqn (5.6)
6. $R \geq T \geq 0 > P \geq S$	SH	<i>C</i> or <i>D</i>	figure 2(b)	eqns (4.1), (4.2)	-
(c) apparent or incidental altruist victim to parasitic manipulation ($0 > R > P$)					
7. $T \geq 0 > R > P \geq S$	PD	<i>D</i> only	figure 2(c)	eqns (4.1), (4.2)	eqn (5.1)
8. $T \geq 0 > R > S > P$	SD	<i>C</i> and <i>D</i>	figure 2(c)	eqns (4.1), (4.2)	eqn (5.1)

576 *Conditions are those in figure 1(a) of $R > P$ and $R > S$ for a social dilemma, which

577 additionally requires $2R > T + S$.

578 **FIGURE LEGENDS**

579

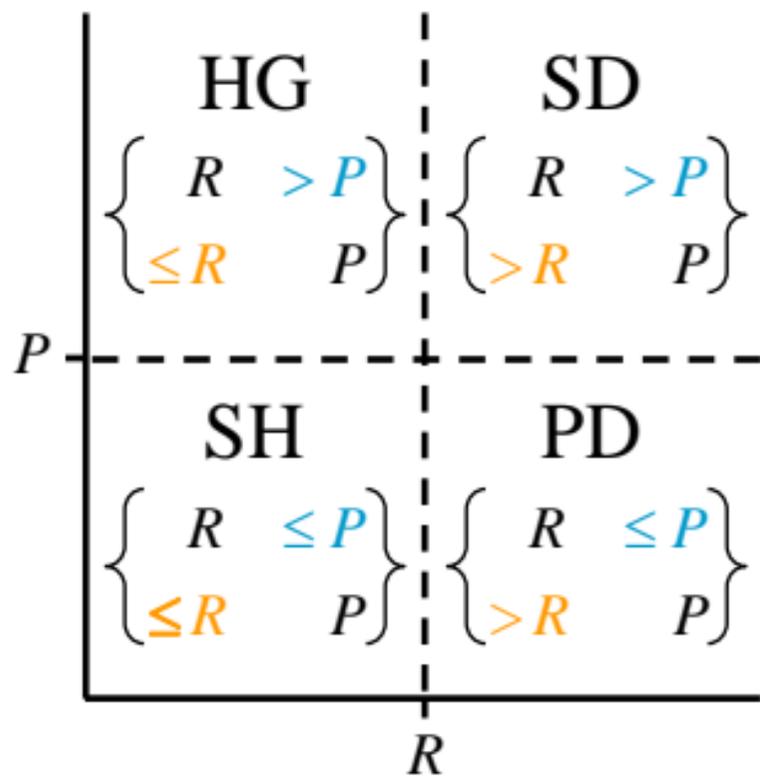
580 Figure. 1. The four canonical games for two strategies on the continuous Temptation-Sucker
581 plane (in gold and blue respectively), calibrated against constant values $R > P$. (a) Conditions
582 on the table-1 payoff matrix for Prisoner's Dilemma (PD), Snow-Drift (SD), Harmony Game
583 (HG), and Stag Hunt (SH). (b) Game outcomes for Cooperator and Defector strategies.

584

585 Figure. 2. Game outcomes as figure 1(b), specifically setting $P = \pm 1/R$. Social dilemmas lie
586 below the angled pink line denoting $2R > S + T$, and $T > R$ or $P > S$, given $R > P$; net-cost
587 fitness transferrals from Cooperator to Defector occur in the stippled +/- quartile. (a) SH
588 takes the origin of the T - S plane (because $R > P \geq 0$, here with $P = 1/R$ and $R = 5/3$). (b) HG
589 takes the origin of the T - S plane ($R \geq 0 > P$, $P = -1/R$ and $R = 3/5$). (c) SD takes the origin of
590 the T - S plane ($0 > R > P$, $P = 1/R$ and $R = -3/5$). (d) SD takes the origin of the α plane for
591 competing genotypes G1 and G2 ($k_1 > k_2 > 0$, here with $k_2/k_1 = 3/5$).

(a)

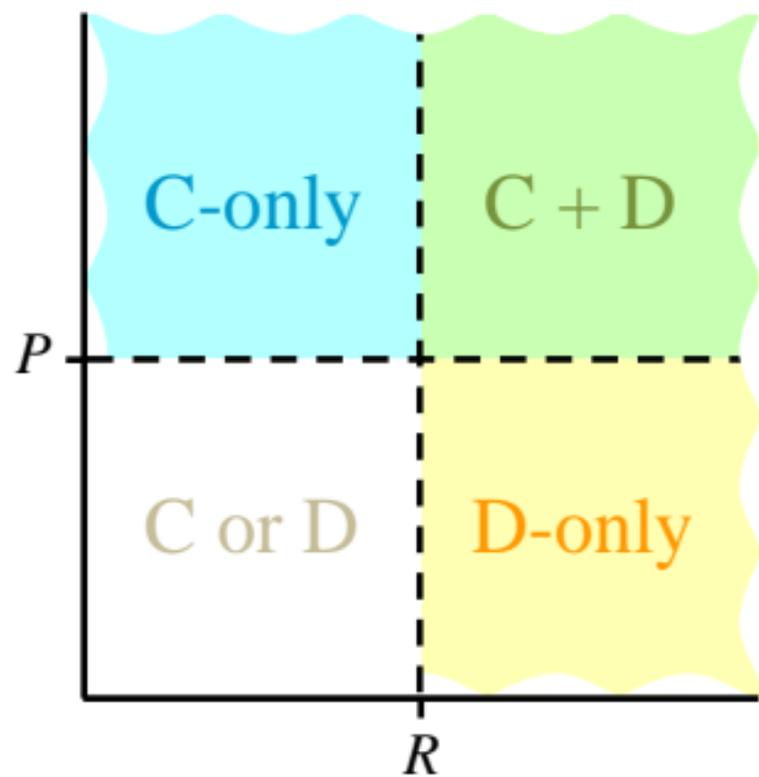
sucker, S



temptation, T

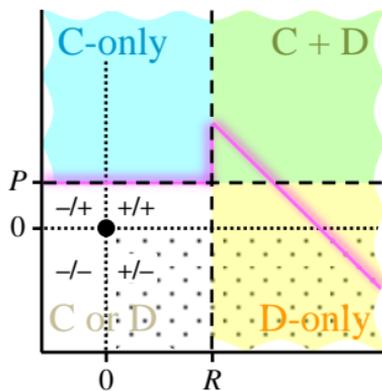
(b)

sucker, S

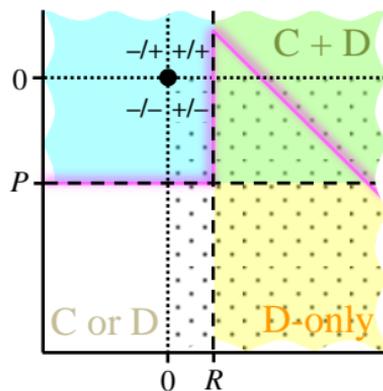


temptation, T

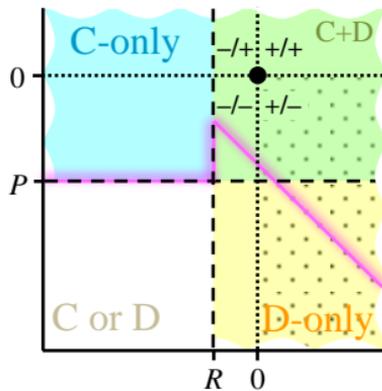
(a)

sucker, S temptation, T

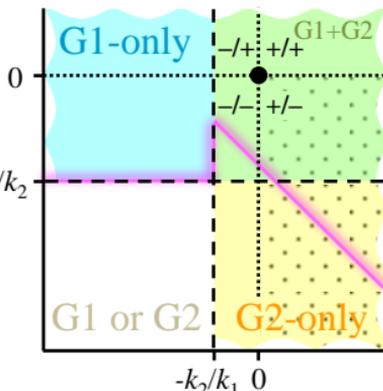
(b)

sucker, S temptation, T

(c)

sucker, S temptation, T

(d)

impact on G1, α_{12} impact on G2, α_{21}