Inclusive fitness and Hamilton's rule in a stochastic environment

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ABSTRACT

The evolution of cooperation in Prisoner's Dilemmas with additive random cost and benefit for cooperation cannot be accounted for by Hamilton's rule based on mean effects transferred from recipients to donors weighted by coefficients of relatedness, which defines inclusive fitness in a constant environment. Extensions that involve higher moments of stochastic effects are possible, however, and these are connected to a concept of random inclusive fitness that is frequency-dependent. This is shown in the setting of pairwise interactions in a haploid population with the same coefficient of relatedness between interacting players. In an infinite population, fixation of cooperation is stochastically stable if a mean geometric inclusive fitness of defection when rare is negative, while fixation of defection is stochastically unstable if a mean geometric inclusive fitness of cooperation when rare is positive, and these conditions are generally not equivalent. In a finite population, the probability for cooperation to ultimately fix when represented once exceeds the probability under neutrality or the corresponding probability for defection if the mean inclusive fitness of cooperation when its frequency is 1/3 or 1/2, respectively, exceeds 1. All these results rely on the simplifying assumption of a linear fitness function. It is argued that meaningful applications of random inclusive fitness in complex settings (multi-player game, diploidy, population structure) would generally require conditions of weak selection and additive gene action.

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1. Introduction

Since its introduction by Hamilton (1964), inclusive fitness has remained one of the main topics in theoretical population biology, but also a subject of controversies (Allen et al., 2013; Frank, 2013; Gardner and West, 2014; Birch and Okasha, 2015; Nowak et al., 2017). The original idea behind the concept of inclusive fitness is to transfer fitness effects of behaviors from recipients to donors weighted by coefficients of relatedness. The concept is best illustrated by Hamilton's rule for the evolution of altruism. The rule states that altruism can evolve if the inequality $-c + rb > 0$ holds, where c is the cost of an altruistic act by a donor, b is the benefit of an altruistic act by a recipient, and r is a coefficient of relatedness between the donor and the recipient. The inequality ensures that the inclusive fitness of an altruistic individual, given by $1 - c + rb$, exceeds the inclusive fitness of a selfish individual, given by 1. Here, we assume only two possible behaviors, altruism and selfishness, and the same coefficient of relatedness between a donor and a recipient. More generally, any number of behaviors and any number of recipients with different coefficients of relatedness between actors and recipients can be considered. Moreover, the inclusive fitness effect of an individual on a baseline value equal to 1 is assumed to be a linear combination of weighted fitness effects of the behavior of this individual on all the individuals affected by this behavior.

Fitness effects used in the original definition of inclusive fitness are additive. This is the case exactly in linear models but only approximately in more general models. Actually, it has been shown that Hamilton's rule with fixed cost, benefit and coefficient of relatedness can predict initial increase and stable fixation of altruism determined at a single locus in random mating populations with any fixed kin-group-structure if the fitness functions are linear (Matessi and Karlin, 1984). In these population genetics models for diploid populations without inbreeding, the coefficient of relatedness at an autosomal locus is given by the expected fraction of genes in the recipient that are identical by descent (i.b.d.) to one or more genes in the donor. More generally, the coefficient of relatedness has been defined as a regression coefficient, and even more generally as a covariance ratio, that can be expressed in terms of identity coefficients or pedigree indices when selection is weak (Hamilton, 1970; Michod and Hamilton, 1980; Uyenoyama, 1984; Grafen, 1985; Lessard, 1992). Under this assumption and with additive gene action on trait value determined at a single locus, it has been shown that inclusive fitness

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can predict if a population strategy is convergence stable (Taylor, 1989a,b) in the sense that a population fixed at a nearby strategy is invaded only by a mutant that brings the population closer to it (Eshel, 1983; Christiansen, 1991).

An alternative approach is to consider that the quantities in Hamilton's rule are not necessarily constants but the best possible approximations at any given time. The favorite candidates are obtained by linear regression, the coefficient of relatedness R being defined as the slope of the regression of the trait value in the recipients on the trait value of the donor, and the cost C and benefit B as the slopes of the regression of the fitness value on the trait values of the donor and recipients, respectively (Queller, 1992; Frank, 1995; Gardner et al., 2011; Rousset, 2015). Note that R, C and B can be viewed as generalized versions of r, c and b, respectively. Then, $-C + RB$ gives the slope of the regression of the fitness value on the trait value, which is positive when the change in the average trait value increases, at least in the case of additive gene action on trait value, owing to the Price covariance formula (Price, 1970). The meaning and scope of this result have been challenged, however, since this is a particular causal interpretation of changes and all quantities are related to each other through the population state including the social interaction structure (Nowak et al., 2017).

Another important issue is the validity of Hamilton's rule under stochastic perturbations. In natural populations, random fluctuations is the rule rather than the exception, and these affect fitness. As recalled by Grafen (1999), stochasticity caused by random fluctuations in population or deme size (demographic stochasticity) is different from stochasticity caused by random fluctuations in selection parameters (environmental stochasticity). Demographic stochasticity can be traced back to an early study of the effect of within-generation variance in offspring number due to Gillespie (1974). It was applied to sex ratio evolution in finite as well as infinite populations (see, e.g., Courteau and Lessard (1999), Lessard (2005)). Since then, demographic fluctuations in subdivided finite populations, mainly island models, have been dealt with using an inclusive fitness approach to kin selection (Rousset and Billiard, 2000; Rousset and Ronce, 2004; Lehmann and Balloux, 2007). See also Taylor et al. (2007), Lessard (2009) for further results on inclusive fitness in finite structured populations. As for environmental stochasticity, refer to Gillespie (1973), Karlin and Levikson (1974), Karlin and Liberman (1974) for early contributions on the effect of between-generation variance in selection parameters, and McNamara (1995), Zheng et al. (2017), Li and Lessard (2020) for more recent studies in the context of evolutionary game theory. This paper deals with implications of these studies on inclusive fitness theory and Hamilton's rule.

In the next sections, we will be addressing the following question: Is there a way to define a concept of random inclusive fitness that accounts for random fitness values in kin selection models? We will try to find the answer in the simplest possible setting, that is, a linear model in a haploid population. This is the case for a Prisoner's Dilemma (PD) with additive random cost and benefit for cooperation in pairwise interactions that occur between cooperators or between defectors in the same proportions as their frequencies with some fixed probability r, and between individuals chosen at random and independently with the complementary probability $1 - r$. Then, the parameter r corresponds to the coefficient of relatedness between interacting individuals and the above question can be addressed. This will be done first in the case of an infinite population with conditions on stochastic local stability of fixation states (Karlin and Liberman, 1974; Zheng et al., 2017, 2018), and second in the case of a finite population with fixation probabilities obtained from a diffusion approximation allowing for random noise in selection

parameters (Karlin and Levikson, 1974; Li and Lessard, 2020). This will be followed by discussion sections on the implications of the results for inclusive fitness and Hamilton's rule in a stochastic environment in more general settings.

2. Randomized PD game in an infinite population

We consider a PD game in an infinite haploid population undergoing discrete, non-overlapping generations with two strategies in use, cooperation (C) and defection (D). In a pairwise interaction between two individuals in the same generation, cooperation by an individual incurs a cost c to the individual and provides a benefit b to the other individual, while defection incurs no cost and provides no benefit. Moreover, cost and benefit are additive so that the payoffs to C and D against C and D, respectively, are given by $b - c$, $-c$, b and 0, respectively. Here, b and c take constant values within each generation but change at random and independently from one generation to another. Finally, interactions occur between individuals chosen at random and independently in the same generation with some fixed probability $1 - r < 1$, and individuals chosen at random but using the same strategy with the complementary probability $r > 0$. This can be achieved by partial sib–sib interactions or partial assortment of strategies. The parameter r can be viewed as a measure of population structure. Here we suppose that r remains constant over successive generations which is a highly simplifying assumption.

In a given generation, let x be the frequency of C so that $1 - x$ is the frequency of D. Then the average payoffs to C and D, respectively, are given by the linear functions $\pi_C(x) = (1 - r)xb + rb - c$ and $\pi_D(x) = (1 - r)xb$. Assuming that cost and benefit are scaled so that the payoff corresponds to a small enough positive or negative change in fitness from a baseline value 1, the frequencies of C and D in the next generation are proportional to $x(1 + \pi_C(x))$ and $(1 - x)(1 + \pi_D(x))$, respectively. Defining $u = x/(1 - x)$, in which case $x = u/(1 + u)$, we get a recurrence equation from the given generation to the next one which can be expressed in the form

$$u' = u \left(\frac{u\alpha + \beta}{u\gamma + \delta} \right), \tag{1}$$

where

$$\begin{pmatrix} \alpha & \beta \\ \gamma & \delta \end{pmatrix} = \begin{pmatrix} 1 - c + b & 1 - c + rb \\ 1 + b - rb & 1 \end{pmatrix}. \tag{2}$$

Note that the same recurrence equation is obtained if the fitnesses of C and D in a two-player game are given by the entries of the above matrix and all pairwise interactions occur at random. This matrix corresponds to an *effective payoff matrix* (Nowak, 2006; Lessard, 2011a).

3. Stochastic local stability conditions

An equilibrium $\hat{x}$ is said to be *stochastically locally stable* (SLS), or more simply *stochastically stable*, if for any $\epsilon > 0$ there exists $\delta_0 > 0$ such that

$$\mathbb{P}\left(x_t \to \hat{x}\right) \geq 1 - \epsilon \quad \text{as soon as} \quad |x_0 - \hat{x}| < \delta_0. \tag{3}$$

This means that the probability for x to tend to $\hat{x}$ over time is as close to 1 as we want if the initial value of x is close enough to $\hat{x}$ (Karlin and Liberman, 1974). On the other hand, $\hat{x}$ is said to be *stochastically locally unstable* (SLU), or more simply *stochastically unstable*, if

$$\mathbb{P}\left(x_t \to \hat{x}\right) = 0 \quad \text{as soon as} \quad |x_0 - \hat{x}| > 0. \tag{4}$$

In this case, $\hat{x}$ cannot be reached with probability 1 from any initial value of x different from $\hat{x}$ (Karlin and Liberman, 1974).

For technical reasons, we assume that α, β, γ and δ in (21) are uniformly bounded below and above by some positive constants, which is the case if the random variables b and c are bounded below and above by some small enough positive constants. Then it can be shown (see Appendix A.1) that the equilibrium $\hat{x} = 0$, which corresponds to D-fixation, is stochastically stable if

$$\mathbb{E}\left(\log\left(1 - c + rb\right)\right) < 0 , \tag{5}$$

and stochastically unstable if the inequality is reversed. Similarly, the equilibrium $\hat{x} = 1$, which corresponds to C-fixation, is stochastically stable if

$$\mathbb{E}\left(\log\left(\frac{1 + b - rb}{1 - c + b}\right)\right)$$
$$= \mathbb{E}\left(\log\left(1 + \frac{c}{1 - c + b} - r\frac{b}{1 - c + b}\right)\right) < 0 , \tag{6}$$

and stochastically unstable if the inequality is reversed.

Note that Hamilton's rule in the form $-c + rb > 0$ almost surely is sufficient for D-fixation to be stochastically unstable and C-fixation to be stochastically stable, but it is generally not necessary unless b and c are constants. Consider, for instance, the case where b and c have expected values, variances and covariance given by $\mu_b s$, $\mu_c s$, $\sigma_b^2 s$, $\sigma_c^2 s$ and $\sigma_{bc} s = \rho\sigma_b\sigma_c s$, respectively, while all higher moments are negligible compared to $s > 0$. Then, a Taylor expansion of the logarithm function yields the approximations

$$\mathbb{E}\left(\log\left(1 - c + rb\right)\right) \approx \left(-\mu_c + r\mu_b - \frac{\sigma_c^2 + r^2\sigma_b^2 - 2r\rho\sigma_b\sigma_c}{2}\right)s \tag{7}$$

and

$$\mathbb{E}\left(\log\left(\frac{1 + b - rb}{1 - c + b}\right)\right)$$
$$\approx \left(\mu_c - r\mu_b + \frac{\sigma_c^2 + (2r - r^2)\sigma_b^2 - 2\rho\sigma_b\sigma_c}{2}\right)s. \tag{8}$$

Therefore, for s small enough, D-fixation is stochastically unstable if the expression in parentheses in (7) is positive, while C-fixation is stochastically stable if the expression in parentheses in (8) is negative. Comparing these two expressions, we conclude that the condition for C-fixation to be stochastically stable implies the condition for D-fixation to be stochastically unstable if $r\sigma_b - \rho\sigma_c > 0$, while it is the opposite if the inequality is reversed.

4. Randomized PD game in a finite population

We now consider a haploid population of finite size N. In anticipation of a diffusion approximation, we assume that the benefit b and cost c for cooperation in any given generation have expected values, variances and covariance given by $\mu_b N^{-1}$, $\mu_c N^{-1}$, $\sigma_b^2 N^{-1}$, $\sigma_c^2 N^{-1}$ and $\sigma_{bc} N^{-1} = \rho\sigma_b\sigma_c N^{-1}$, respectively, while all higher moments are negligible compared to N^{-1}. Such a scaling for temporally varying selection parameters can be traced back to Karlin and Levikson (1974). It is in agreement with the scaling in the previous section with s instead of N^{-1} and makes the variability in selection parameters not to vanish in the limit of a large population size.

Let the frequency of C in a given generation be x and the frequency of C in the next generation be x'. Assuming a Wright–Fisher model with pairwise interactions occurring among an infinite number of offspring, the random variable $x'N$ follows a conditional binomial distribution with parameters N and

$$\tilde{x} = \frac{x(1 + \pi_C(x))}{1 + x\pi_C(x) + (1 - x)\pi_D(x)}. \tag{9}$$

Taking N generations as unit of time, the difference $\Delta x = x' - x$ is the change in the frequency of C from time t corresponding to the given generation to time $t + \Delta t$ corresponding to the next generation with $\Delta t = N^{-1}$. Calculations (see Appendix A.2) show that the moments of Δx satisfy $\mathbb{E}(\Delta x) \approx m(x)\Delta t$, where

$$m(x) = x(1 - x)\left(-\mu_c + r\mu_b - x(\sigma_c^2 + r^2\sigma_b^2 - (1 + r)\rho\sigma_b\sigma_c)\right), \tag{10}$$

and $\mathbb{E}((\Delta x)^2) \approx v(x)\Delta t$, where

$$v(x) = x(1 - x)\left(1 + x(1 - x)(\sigma_c^2 + r^2\sigma_b^2 - 2r\rho\sigma_b\sigma_c)\right), \tag{11}$$

while $\mathbb{E}((\Delta x)^4)$ is negligible compared to Δt. These properties characterize a diffusion approximation with drift function $m(x)$ and diffusion function $v(x)$ in the limit of a large population size.

5. Fixation probabilities

In the diffusion approximation, it is known (Ewens, 2004; Li and Lessard, 2020) that the probability of ultimate fixation of C from an initial frequency N^{-1} is given by

$$F_C = \left(N\int_0^1 \exp\left(-2\int_0^y \frac{m(x)}{v(x)}dx\right)dy\right)^{-1}. \tag{12}$$

Similarly, the probability of ultimate fixation of D from an initial frequency N^{-1} is given by

$$F_D = \left(N\int_0^1 \exp\left(2\int_y^1 \frac{m(x)}{v(x)}dx\right)dy\right)^{-1}. \tag{13}$$

Since the probability of ultimate fixation in the absence of selection is equal to the initial frequency, the evolution of cooperation is said to be *favored by selection* if $F_C > N^{-1}$ (Nowak et al., 2004). Analogously, the evolution of cooperation is *more favored by selection* than the evolution of defection if $F_C > F_D$, while the evolution of defection is *disfavored by selection* if $F_D < N^{-1}$. Note that the condition for $F_C > F_D$ in the absence of mutation coincides with the condition for the average abundance of C to exceed the average abundance of D in the stationary state under symmetric recurrent mutation in the limit of a low mutation rate (Rousset and Billiard, 2000; Rousset, 2003; Fudenberg and Imhof, 2006).

Under the assumption that the scaled expected values and variances of the payoffs, μ_b, μ_c, σ_b^2 and σ_c^2, are small enough, it can be shown (see Appendix A.2) that the conditions for $F_C > N^{-1}$, $F_C > F_D$ and $F_D < N^{-1}$ reduce in the case at hand to

$$-\mu_c + r\mu_b - x_0\left(\sigma_c^2 + r^2\sigma_b^2 - (1 + r)\rho\sigma_b\sigma_c\right) > 0 \tag{14}$$

for $x_0 = 1/3$, $1/2$ and $2/3$, respectively. Therefore, if $\sigma_c^2 + r^2\sigma_b^2 - (1 + r)\rho\sigma_b\sigma_c > 0$ holds, then $F_C > N^{-1}$ is implied by $F_C > F_D$ which is implied by $F_D < N^{-1}$, while the implications are in the opposite direction if the inequality is reversed.

6. Implications for inclusive fitness and Hamilton's rule

When the additive cost and benefit for cooperation in a Prisoner's Dilemma (PD) are constant, which means that they are given by their expected values $\mu_b s$ and $\mu_c s$, since then their variances $\sigma_b^2 s$ and $\sigma_c^2 s$ vanish, Hamilton's rule for the evolution of cooperation takes the form $-\mu_c + r\mu_b > 0$, where r is the coefficient of relatedness between two interacting individuals. In an infinite haploid population, this is the condition for cooperation to be stochastically locally stable, actually deterministically locally stable, and defection to be stochastically locally unstable, actually deterministically locally unstable. In a haploid population of fixed finite size N, this is also the condition for selection to

favor the evolution of cooperation ($F_C > N^{-1}$), favor more the evolution of cooperation than the evolution of defection ($F_C > F_D$), and disfavor the evolution of defection ($F_D < N^{-1}$). Then, Hamilton's rule fully accounts for the evolution of cooperation based on local stability properties in an infinite population or fixation probabilities in a finite population. Actually, this conclusion holds for structured haploid populations as long as fitness effects are small, constant and additive (Rousset and Billiard, 2000; Taylor et al., 2007; Ohtsuki, 2010; Lessard, 2011a,b).

When the cost c and benefit b for cooperation are not constant, however, not only the conditions for the above evolutionary properties do not reduce to $r\mu_b - \mu_c > 0$, but they are all different. The main reasons appear to be that inclusive fitness is a relative concept and that the expected value of a non-linear function of a random variable is generally not equal to this function evaluated at the expected value of the random variable.

The expression $1 - c + rb$ seems to be suitable for the inclusive fitness of C in an all D population with the fitness of D set equal to 1. But then, what would be a suitable expression for the inclusive fitness of D in an all C population with the fitness of C set equal to 1? It occurs that it is not $1/(1 - c + rb)$, but rather $1 + c/(1 - c + b) - rb/(1 - c + b)$, where $c/(1 - c + b)$ represents the benefit for defection and $b/(1 - c + b)$ its cost. Not only these benefit and cost are non-linear functions with respect to b and c, but benefit and cost depend on the population state even in the simplest setting.

7. Geometric mean inclusive fitness

The stochastic local stability or instability of D-fixation in an infinite population following the introduction of C does not rely on the sign of the expected value of the random variable $1 - c + rb$, which is $1 - \mu_c s + r\mu_b s$ where $\mu_b s$ and $\mu_c s$ are the expected values of b and c, respectively. It rather depends on the sign of the expected value of its logarithm, which happens not to be $\log(1 - \mu_c s + r\mu_b s)$ since the logarithm function is non-linear. Actually, with $\sigma_b^2 s$ and $\sigma_c^2 s$ being the variances b and c, and $\rho\sigma_b\sigma_c s$ their covariance, while all higher moments are of smaller order, the expected value of $\log(1 - c + rb)$ is approximated by $\left(-\mu_c + r\mu_b + (\sigma_c^2 + r^2\sigma_b^2 - 2r\rho\sigma_b\sigma_c)/2\right) s$. This expected value represents the geometric mean selective advantage or disadvantage of C near D-fixation and, by analogy with the concept of geometric mean fitness (Ewens, 2004), it can be called its *geometric mean inclusive fitness*.

Then, the condition for D-fixation to be stochastically unstable is that the geometric mean inclusive fitness of C near D-fixation is positive, which reduces to

$$-\mu_c + r\mu_b - \frac{\sigma_c^2 + r^2\sigma_b^2 - 2r\rho\sigma_b\sigma_c}{2} > 0. \tag{15}$$

This is the condition for non extinction of C with probability 1 following its introduction. This condition is related to the condition for initial increase of C in the deterministic case and, more generally, to the use of inclusive fitness to determine convergence stable strategies (Taylor, 1989a,b). It can be seen as an extension of Hamilton's rule for the evolution of cooperation in a stochastic environment. Note, however, that this is not the condition for C-fixation to be stochastically stable, given by

$$\mu_c - r\mu_b + \frac{\sigma_c^2 + (2r - r^2)\sigma_b^2 - 2\rho\sigma_b\sigma_c}{2} > 0, \tag{16}$$

which is the condition for the geometric mean inclusive fitness of D near C-fixation to be negative.

8. Frequency-dependent inclusive fitness

In a finite population, fixation probabilities depend on all possible population states from the initial state up to fixation. In a diffusion approximation, these probabilities are expressed in terms of integrals that involve the drift and diffusion functions. These in turn depend on the first and second scaled moments of b and c. In particular, the drift function $m(x)$ in (10), which gives the conditional expected rate of change of C frequency, is positive for $0 < x < 1$ if and only if

$$-\mu_c + r\mu_b - x\left(\sigma_c^2 + r\sigma_b^2 - (1+r)\rho\sigma_b\sigma_c\right) > 0. \tag{17}$$

This is the condition for the expected value of the function

$$\varphi_C(x) = 1 - \frac{c(1-x)}{1+(b-c)x} + r\frac{b(1-x)}{1+(b-c)x} \tag{18}$$

to exceed 1 in a large enough population. This expression can be interpreted as the inclusive fitness of C when its frequency in the population is x. In this interpretation, $c(1-x)/(1+(b-c)x)$ and $b(1-x)/(1+(b-c)x)$ represent the cost and benefit, respectively, of substituting one individual chosen at random with a C individual. These cost and benefit are inversely proportional to the current average fitness in the population given by $1+(b-c)x$. This agrees with the previous expressions for inclusive fitness when $x = 0$ or $x = 1$.

Note that the inclusive fitness effect of C satisfies

$$\varphi_C(x) - 1 = \frac{(1-x)(\pi_C(x) - \pi_D(x))}{1 + x\pi_C(x) + (1-x)\pi_D(x)}. \tag{19}$$

Therefore, saying that the expected value of $\varphi_C(x)$ exceeds 1 is an alternative way of saying that the expected value of the expression on the right-hand side of the above equation is positive. Moreover, we have $x' = x\varphi_C(x)$ from one generation to the next so that the inclusive fitness of C is an expression for the geometric growth factor of C frequency in discrete time, while the inclusive fitness effect of C is an expression for the corresponding exponential growth rate in continuous time.

If b and c are constant with scaled values μ_b and μ_c satisfying $r\mu_b - \mu_c > 0$, then the conditional expected rate of change in the frequency of C is always positive. In this case, it is not surprising that the probability of ultimate fixation of a single C exceeds its initial frequency ($F_C > N^{-1}$) as well as the probability of ultimate fixation of a single D by symmetry ($F_C > F_D$), which is itself less than its initial frequency ($F_D < N^{-1}$). In the general case, the scaled variances of the payoffs and their correlation coefficient can change the sign of the drift function with respect to the frequency of C. Then, the conditions for $F_C > N^{-1}$, $F_C > F_D$ and $F_D < N^{-1}$ are no longer the same. When the scaled first and second moments of the payoffs are small, these conditions turn out to be that the mean inclusive fitness of C exceeds 1 when its frequency in a large population is 1/3, 1/2 and 2/3, respectively. The first and last conditions are related to the one-third law of evolution and the middle one to the concept of risk dominance (Nowak et al., 2004; Lessard, 2005; Imhof and Nowak, 2006; Ohtsuki et al., 2006; Lessard, 2011b). They are all consequences of the fact that the expected inclusive fitness of C in a large population is a linear function of the frequency of C. It is worth noting, however, that these conditions have been obtained under the assumption of small scaled first and second moments of the payoffs, which is more restrictive than the mere assumption of weak selection.

9. Public goods game in a diploid population

A diploid population with additive gene action is similar to a haploid population, and a public goods game in the form of a

linear n-player Prisoner's Dilemma (Archetti and Scheuring, 2012) similar to a two-player game. This is the case with two alleles C and D so that CC individuals always cooperate, DD individuals always defect, and CD individuals cooperate or defect with the same probability $1/2$, and with groups of n individuals so that cooperation incurs a cost $2c$ to the individual but provides a benefit $2b$ equally shared among all the other individuals in the same group. Assuming random mating and groups of n offspring formed so that the coefficient of relatedness between two off-spring in the same group is constant and given by r, it can be shown (see Appendix A.3) that the inclusive fitnesses of C and D take the previous forms with $1 + 2(b - c)x$ instead of $1 + (b - c)x$ as average fitness when the frequency of C is x. This holds when b and c are constants as well as random variables.

10. Generalized Hamilton's rule

In a generalized version of Hamilton's rule (Queller, 1992; Frank, 1995; Gardner et al., 2011; Rousset, 2015), cost and benefit of a trait under selection in a constant environment have been defined as the slopes of the plane obtained by least squares regression of fitness on the trait value of an individual and the average trait value of its partners, denoted by C and B, respectively. Then the change in the average trait value can be expressed as the variance of the trait value times $-C + RB$ divided by the average fitness, where R is the slope of the least squares regression line of the average trait value of an individual's partners on the trait value of the individual. This leads to the generalized Hamilton's rule $-C + RB > 0$ for an increase in the average trait value.

As it is often the case with least squares methods, the interpretation of the generalized Hamilton's rule can be criticized (Allen et al., 2013; Nowak et al., 2017). Not only is the form of the expression predetermined, but all three quantities in it are summary statistics of the entire population state and structure. In the simplified haploid model that we have considered where the trait value is the frequency of C, that is, 1 for a C individual and 0 otherwise, the quantities C, B and R correspond to c, b and r, respectively, which are *a priori* defined independently of the population state as cost, benefit and coefficient of relatedness, respectively. In general, however, these quantities depend on the joint probability distribution of trait value and average trait value of partners in the whole population, and their meaning beyond the analogy with a simplified model is unclear. This would be all the more so in a stochastic environment with a condition for an increase in the expected average trait value that could be expressed, by extending our results, as $-\mathbb{E}(C) + R\,\mathbb{E}(B)$ large enough, actually larger than some function of variances and co-variances of fitness values under the assumption of small random perturbations over successive generations.

In addition, the generalized Hamilton's rule requires that the trait value is linear with respect to type frequencies so that its average change is given by the covariance between the trait value and fitness divided by the average fitness, which is known as the Price covariance formula (Price, 1970; Frank, 1995). In a population genetics framework, this situation corresponds to additive gene action on trait value. In general, the change in an average trait value in a diploid population is not given by this formula but only approximated under weak selection by the additive genetic covariance divided by the average fitness (Nagylaki, 1993). This is known as the asymptotic secondary theorem of natural selection. Without the assumption of weak selection, this approximation can be considered as a partial change in average trait value, but then its interpretation is as controversial as Fisher's (Fisher, 1930) fundamental theorem for the change in average fitness (Price, 1972; Ewens, 1989; Lessard, 1997; Edwards, 2002; Ewens and Lessard, 2015; Grafen, 2018; Lessard and Ewens, 2019).

11. Further remarks

It may look surprising that the drift function in a diffusion approximation for a strategy frequency in a finite population is determined by a mean inclusive fitness, while the stochastic local stability or instability of a fixation state in an infinite population depends on a geometric mean inclusive fitness. The reason may be that the recurrence equation from one generation to the next one involved in the latter case makes it a multiplicative model, while random sampling in each generation in the former case makes it an additive model. When inclusive fitness is deterministic, its mean is larger than 1 if and only if its geometric mean is positive. When inclusive fitness is stochastic, this is not generally the case. It was pointed out in McNamara (1995), Grafen (1999) that a geometric mean fitness in a stochastic environment is maximized when an arithmetic mean reproductive value is maximized. The exact meaning of this property and its implication for inclusive fitness remain to be examined.

Being frequency-dependent, inclusive fitness in a stochastic environment as well as in a deterministic environment can be best used to study local dynamic properties such as evolutionary stability (Maynard Smith and Price, 1973; Maynard Smith, 1974), convergence stability (Eshel, 1983, 1996; Christiansen, 1991; Rousset, 2003) and neighborhood invasibility (Apaloo, 1997). Moreover, let us recall that inclusive fitness was originally introduced in a population genetics framework as an alternative linear function that accounts for a linear neighbor modulated fitness function (Hamilton, 1964). This is tantamount to the validity of Hamilton's rule under weak selection. Then, identity measures between interacting individuals converge rapidly, while type frequencies change slowly. With further additivity assumptions on fitness or trait value, these two timescales make possible meaningful inclusive fitness formulations as shown at least for populations structured in families, groups or demes in a deterministic environment (Matessi and Karlin, 1984; Uyenoyama, 1984; Lessard and Rocheleau, 2004; Taylor et al., 2007; Ohtsuki, 2010; Lessard, 2011a). Under weak selection without additivity assumptions, inclusive fitness formulations may still be possible by introducing extended identity measures but then they become intricate and difficult to interpret (see, e.g., Lessard (1992, 2009) and references therein). Not to mention that, in the case of age-structured populations and more generally class-structured populations, there are disagreements on the definition of fitness itself, and *a fortiori* on the definition of inclusive fitness, based on reproductive values (Grafen, 2015a,b; Lessard and Soares, 2016, 2018; Soares and Lessard, 2020). In all cases, there are conditions for inclusive fitness to capture the direction of evolution and these generally go beyond local approximations.

Another view is to consider that, like Fisher (1930) fundamental theorem, the inclusive fitness effect is actually a partial effect as best predicted by least squares from the genes present at any given time in a population in a constant environment including a constant genic environment. But then, inclusive fitness captures only one aspect of evolution, the one concerned with the instantaneous effect of gene frequency changes under the constraint that the population structure is unchanged, and its biological meaning in general settings remains unclear.

12. Summary

In two-player Prisoner's Dilemmas with a fixed coefficient of relatedness r between players and additive random cost c and benefit b for cooperation, stochastic local stability of cooperation once fixed in an infinite population depends on the sign of a geometric mean inclusive fitness of defection in an all cooperating population. This sign can be different from the sign of

the geometric mean inclusive fitness of cooperation in an all defecting population that determines stochastic local instability of defection. The geometric mean inclusive fitness is not linear with respect to mean cost and benefit unless cost and benefit are constant. Moreover, these generally depend on the population state. In a population of large finite size under weak selection, the probability of ultimate fixation of cooperation when introduced as a single mutant exceeds what it would be under neutrality if the mean inclusive fitness of cooperation when its frequency is $1/3$ exceeds 1. Moreover, this fixation probability for cooperation exceeds the corresponding one for defection if the mean inclusive fitness of cooperation when its frequency is $1/2$ exceeds 1. These provide new interpretations of the one-third law of evolution and risk dominance, respectively. The conditions obtained for the evolution of cooperation depend on higher moments of cost and benefit in different ways, and each one can be considered as an extension of Hamilton's rule for the evolution of cooperation when additive cost and benefit are constant. The results apply as well to a multi-player public goods game in a diploid population with additive gene action. They shed light on possible inclusive fitness formulations in populations in a stochastic environment under conditions of weak selection and additive gene action.

CRediT authorship contribution statement

Sabin Lessard: Revised all the results and applied them to inclusive fitness. **Cong Li:** Calculated fixation probabilities in a finite population. **Xiu-Deng Zheng:** Worked mainly on conditions for stochastic stability in an infinite population. **Yi Tao:** Initiated the study on evolutionary games in a stochastic environment.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix

A.1. Stochastic local stability in two-player games

With pairwise interactions in an infinite haploid population undergoing discrete, nonoverlapping generations, and two strategies in use, C and D, let α_k, β_k, γ_k and δ_k be the fitnesses of C and D in interaction with C and D, respectively, in generation k. We assume throughout that the fitnesses in different generations are independent random variables that have the same joint probability distribution. Moreover, they are uniformly bounded below and above by some positive constants. Assuming random pairwise interactions within generation, the frequency of C from generation k to generation $k + 1$ is given by

$$x_{k+1} = \frac{x_k^2 \alpha_k + x_k(1 - x_k)\beta_k}{x_k^2 \alpha_k + x_k(1 - x_k)(\beta_k + \gamma_k) + (1 - x_k)^2 \delta_k}. \tag{20}$$

Introducing the ratio $u_k = x_k/(1 - x_k)$, we have the recurrence equation

$$u_{k+1} = u_k \left(\frac{u_k \alpha_k + \beta_k}{u_k \gamma_k + \delta_k} \right), \tag{21}$$

which can be written in the form

$$\frac{u_{k+1}}{u_k} = \frac{\beta_k}{\delta_k} \left(1 + \frac{u_k(\alpha_k \delta_k - \beta_k \gamma_k)}{u_k \beta_k \gamma_k + \beta_k \delta_k} \right), \tag{22}$$

from which

$$\frac{1}{n} \log \left(\frac{u_n}{u_0} \right) = \frac{1}{n} \sum_{k=0}^{n-1} \log \left(\frac{\beta_k}{\delta_k} \right) + \frac{1}{n} \sum_{k=0}^{n-1} \log \left(1 + \frac{u_k(\alpha_k \delta_k - \beta_k \gamma_k)}{u_k \beta_k \gamma_k + \beta_k \delta_k} \right). \tag{23}$$

Defining

$$\mu = \mathbb{E} \left(\log \left(\frac{\beta_k}{\delta_k} \right) \right), \tag{24}$$

the strong law of large numbers and Egorov's theorem guarantee that

$$\frac{1}{n} \sum_{k=0}^{n-1} \log \left(\frac{\beta_k}{\delta_k} \right) \to \mu \tag{25}$$

with probability 1, the convergence being uniform on a sample set of probability as close to 1 as we want. A finer analysis that takes into account the second term on the right-hand side in (23) under the above assumptions (Karlin and Liberman, 1975; Zheng et al., 2017) shows that

$$\frac{1}{n} \log \left(\frac{u_n}{u_0} \right) \to \mu \tag{26}$$

with probability 1 if $\mu > 0$ and $u_0 > 0$, and with probability as close to 1 as we want if $\mu < 0$ and u_0 is small enough. In the former case, we have $u_n \nrightarrow 0$ with probability 1, and then D-fixation is stochastically locally unstable (SLU), while in the latter case, we have $u_n \to 0$ with probability as close to 1 as we want, and then D-fixation is stochastically locally stable (SLS). Similarly, defining

$$\nu = \mathbb{E} \left(\log \left(\frac{\gamma_k}{\alpha_k} \right) \right), \tag{27}$$

we have that C-fixation is stochastically locally unstable if $\nu > 0$ and stochastically locally stable if $\nu < 0$.

A.2. Diffusion approximation for two-player games with random payoffs

Let the average fitnesses of C and D in random pairwise interactions among offspring produced in large number be in the form $1 + \pi_C(x)$ and $1 + \pi_D(x)$ when the frequency of C is x in the parental generation of a haploid population of fixed finite size N undergoing discrete, nonoverlapping generations according to a Wright–Fisher model. Here, we assume that the average payoff functions $\pi_C(x)$ and $\pi_D(x)$ are random variables of expected values, variances and covariance given by $\mu_C N^{-1}$, $\mu_D N^{-1}$, $\sigma_C^2 N^{-1}$, $\sigma_D^2 N^{-1}$ and $\sigma_{CD} N^{-1}$, respectively, which actually all depend on x, while all higher moments are functions $o(N^{-1})$. We note that the frequency of C in the next generation times N follows a conditional binomial probability distribution of parameters N and

$$\tilde{x} = \frac{x(1 + \pi_C(x))}{1 + x\pi_C(x) + (1 - x)\pi_D(x)}. \tag{28}$$

Moreover, using the central moments of this conditional distribution, the first and second moments of $\Delta x = x' - x$, which represents the change in the frequency of C, can be expressed as

$$\mathbb{E}(\Delta x) = \mathbb{E}\left((x' - \tilde{x}) + (\tilde{x} - x)\right) = \mathbb{E}(\tilde{x} - x) \qquad (29)$$

and

$$\mathbb{E}((\Delta x)^2) = \mathbb{E}\left((x' - \tilde{x})^2 + (\tilde{x} - x)^2\right) = \mathbb{E}\left(\frac{\tilde{x}(1 - \tilde{x})}{N} + (\tilde{x} - x)^2\right). \qquad (30)$$

Then, considering the power series of $\tilde{x}$ in $\pi_C(x)$ and $\pi_D(x)$, the assumptions on the moments of these variables lead to

$$\mathbb{E}(\Delta x) = \frac{x(1 - x)}{N}\left(\mu_C - \mu_D - x\sigma_C^2 - (1 - 2x)\sigma_{CD} + (1 - x)\sigma_D^2\right) + o(N^{-1}) \qquad (31)$$

and

$$\mathbb{E}((\Delta x)^2) = \frac{x(1 - x)}{N}\left(1 + x(1 - x)(\sigma_C^2 - 2\sigma_{CD} + \sigma_D^2)\right) + o(N^{-1}). \qquad (32)$$

Similarly, the fourth moment can be expressed as

$$\mathbb{E}((\Delta x)^4) = \mathbb{E}\left((x' - \tilde{x})^4 + 4(x' - \tilde{x})^3(\tilde{x} - x) + 6(x' - \tilde{x})^2(\tilde{x} - x)^2 + (\tilde{x} - x)^4\right), \qquad (33)$$

from which

$$\mathbb{E}((\Delta x)^4) = \mathbb{E}\left(\frac{\tilde{x}(1 - \tilde{x})}{N}\left(\frac{1 + (3N - 6)\tilde{x}(1 - \tilde{x})}{N^2}\right.\right.$$
$$\left.\left. + \frac{4(\tilde{x} - x)^2(1 - 2\tilde{x})}{N} + 6(\tilde{x} - x)\right)\right)$$
$$+ \mathbb{E}\left((\tilde{x} - x)^4\right), \qquad (34)$$

which is a function $o(N^{-1})$. In the limit of a large population with N generations as unit of time (Kimura, 1964; Karlin and Levikson, 1974; Karlin and Taylor, 1981; Ewens, 2004; Li and Lessard, 2020), these conditions characterize a diffusion approximation with

$$m(x) = x(1 - x)\left(\mu_C - \mu_D - x\sigma_C^2 - (1 - 2x)\sigma_{CD} + (1 - x)\sigma_D^2\right) \qquad (35)$$

as drift function and

$$v(x) = x(1 - x)\left(1 + x(1 - x)\left(\sigma_C^2 - 2\sigma_{CD} + \sigma_D^2\right)\right) \qquad (36)$$

as diffusion function.

When the average payoff functions are in the form

$$\pi_C(x) = x(1 - r)b + rb - c, \qquad \pi_D(x) = x(1 - r)b, \qquad (37)$$

where b and c represent benefit and cost for cooperation that have expected values, variances and covariance given by $\mu_b N^{-1}$, $\mu_c N^{-1}$, $\sigma_b^2 N^{-1}$, $\sigma_c^2 N^{-1}$ and $\rho\sigma_b\sigma_c N^{-1}$, respectively, while all higher moments are functions $o(N^{-1})$, calculations lead to a diffusion approximation with drift and diffusion functions given by

$$m(x) = x(1 - x)(-\mu_c + r\mu_b - x(\sigma_c^2 + r\sigma_b^2 - (1 + r)\rho\sigma_b\sigma_c)) \qquad (38)$$

and

$$v(x) = x(1 - x)\left(1 + x(1 - x)(\sigma_c^2 + r^2\sigma_b^2 - 2r\rho\sigma_b\sigma_c)\right), \qquad (39)$$

respectively. The probability of ultimate fixation of C from a small initial frequency N^{-1} is given by

$$F_C = \frac{\psi(0)}{N\int_0^1 \psi(y)dy}, \qquad (40)$$

where

$$\psi(y) = \exp\left(-2\int_0^y \frac{m(x)}{v(x)}dx\right). \qquad (41)$$

Assuming μ_b, μ_c, σ_b^2 and σ_c^2 small enough, we have the approximation

$$\psi(y) \approx 1 - 2\int_0^y (-\mu_c + r\mu_b - x(\sigma_c^2 + r\sigma_b^2 - (1 + r)\rho\sigma_b\sigma_c))dx, \qquad (42)$$

from which

$$F_C \approx N^{-1}\left(1 - \mu_c + r\mu_b - \frac{1}{3}\left(\sigma_c^2 + r\sigma_b^2 - (1 + r)\rho\sigma_b\sigma_c\right)\right). \qquad (43)$$

Similarly, the probability of ultimate fixation of D from a small initial frequency N^{-1} is given by

$$F_D = \frac{\psi(1)}{N\int_0^1 \psi(y)dy}, \qquad (44)$$

and approximated by

$$F_D \approx N^{-1}\left(1 + \mu_c - r\mu_b + \frac{2}{3}\left(\sigma_c^2 + r\sigma_b^2 - (1 + r)\rho\sigma_b\sigma_c\right)\right). \qquad (45)$$

A.3. Multi-player game in a randomly mating diploid population

We consider here a diploid population under random mating in which C and D are two alleles segregating at a single locus. These alleles have additive effects on the expression of cooperation so that CC individuals cooperate, DD individuals defect, and CD individuals cooperate half of the time and defect the other half of the time. The model of interaction between individuals is a public goods game that takes the form of a linear n-player Prisoner's Dilemma (Archetti and Scheuring, 2012). Interactions occur within groups of n individuals in which cooperation by a focal individual incurs a cost $2c$ to this individual but provides a benefit $2b$ equally shared by its $n - 1$ partners in the same group. Groups are formed at random but with assortment so that, with a fixed probability r and independently from one another, any maternal or paternal gene in any partner is identical to the corresponding gene in the focal individual, while it is chosen at random and independently in the whole population with the complementary probability $1 - r$. This ensures that the coefficient of relatedness between a focal individual and any of its parters in the same group is r. This is the case, for instance, if each group is obtained by random sampling in a mixed pool of offspring produced by the same parental pair and offspring produced by all parental pairs (Matessi and Karlin, 1984). Finally, the effects of cooperation on each member of a group are added to get its payoff.

Under the above assumptions, the average payoffs to D and C are given by $\pi_D(x) = x(-c - rb + 2b)$ and $\pi_C(x) = -c + rb + \pi_D(x)$, respectively, where x is the current frequency of C. Taking $1 + \pi_D(x)$ and $1 + \pi_C(x)$ as fitnesses of C and D, respectively, the dynamics for $u = x/(1 - x)$ in an infinite population undergoing discrete, nonoverlapping generations obeys the recurrence equation

$$u' = u\left(\frac{u\alpha + \beta}{u\gamma + \delta}\right), \qquad (46)$$

where

$$\begin{pmatrix} \alpha & \beta \\ \gamma & \delta \end{pmatrix} = \begin{pmatrix} 1 - 2c + 2b & 1 - c + rb \\ 1 - c + 2b - rb & 1 \end{pmatrix}. \qquad (47)$$

With random cost and benefit, the analysis in the first section shows that D-fixation is stochastically locally unstable if

$$\mathbb{E}\left(\log\left(1 - c + rb\right)\right) > 0 \,, \tag{48}$$

while C-fixation is stochastically locally stable if

$$\mathbb{E}\left(\log\left(\frac{1 - c + 2b - rb}{1 - 2c + 2b}\right)\right)$$
$$= \mathbb{E}\left(\log\left(1 + \frac{c}{1 - 2c + 2b} - r\frac{b}{1 - 2c + 2b}\right)\right) < 0 \,. \tag{49}$$

On the other hand, with random cost and benefit satisfying the same assumptions as in the previous section in a population of large finite size N, the frequency of C is described by a diffusion approximation with

$$m(x) = x(1 - x)(-\mu_c + r\mu_b - 2x(\sigma_c^2 + r\sigma_b^2 - (1 + r)\rho\sigma_b\sigma_c)) \tag{50}$$

as drift function, and

$$v(x) = x(1 - x)\left(1 + x(1 - x)(\sigma_c^2 + r^2\sigma_b^2 - 2r\rho\sigma_b\sigma_c)\right) \tag{51}$$

as diffusion function. If μ_b, μ_c, σ_b^2 and σ_c^2 are small enough, then the probability of ultimate fixation of a rare allele C or D exceeds its initial frequency if and only if $m(1/3) > 0$ or $m(2/3) > 0$, respectively, while the former exceeds the latter if and only if $m(1/2) > 0$. Moreover, $m(x) > 0$ for $0 < x < 1$ if and only if

$$\mathbb{E}\left(\frac{(1 - x)(\pi_C(x) - \pi_D(x))}{1 + x\pi_C(x) + (1 - x)\pi_D(x)}\right)$$
$$= \mathbb{E}\left(1 - \frac{c(1 - x)}{1 + 2(b - c)x} + r\frac{b(1 - x)}{1 + 2(b - c)x}\right) > 1. \tag{52}$$

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