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The asymmetry between spite and altruism

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ABSTRACT

Empirical evidence suggests that altruistic social behavior (helping others at a cost to oneself) is more common than spiteful behavior (harming others at a cost to oneself) in nature. Here, we provide a general mathematical explanation for this asymmetry based on fundamental constraints on the composition of social groups. Since both behaviors are costly to the actor, they require additional mechanisms to avoid being eliminated by natural selection, such as assortative interactions. When interactions tend to occur between similar individuals (positive assortment), altruism can evolve, whereas spite requires negative assortment. We use a linear game in groups of fixed size n to derive an index of assortativity, and we analyze evolution in both infinite and finite populations. We show that positive assortment faces no fundamental limits – complete segregation into homogeneous groups is always mathematically possible. In contrast, negative assortment is constrained, especially in larger groups and unbalanced populations. This asymmetry creates more opportunities for altruism to evolve than spite. Our results explain the empirical rarity of spiteful behavior without assuming any specific population structure or group formation mechanism, suggesting that the scarcity of spite may reflect fundamental mathematical constraints inherent to assortment patterns.

1. Introduction

Social behaviors can be categorized into four types based on the positive or negative effects that they have on actors and recipients (Hamilton, 1964a, 1964b). These four social behaviors are altruistic behavior, spiteful behavior, mutualistic behavior, and selfish behavior. Altruistic behavior, which is costly to the actor but beneficial to the recipient, and spiteful behavior, which is costly to both the actor and the recipient, are expected to be eliminated by natural selection. Therefore, their existence requires explanation (Hamilton, 1964a, 1964b, 1970).

If individuals are more likely to encounter others of the same type than what would be expected only by chance, altruistic behavior can evolve (Hamilton, 1964a, 1964b; Eshel and Cavalli-Sforza, 1982; Fletcher and Doebeli, 2009). Conversely, if encounters with individuals of the same type are rare, spiteful behavior can evolve (Hamilton, 1970, 1971; Foster et al., 2001; Gardner and West, 2004; West and Gardner, 2010; Smead and Forber, 2013; Madgwick, 2020). One mechanism that enables such an evolution is known as the green-beard effect, as described by Hamilton (1964a, 1964b) in its introduction to kin selection theory (see Maynard Smith, 1964, and Dawkins, 1976, for further details). If individuals with green beards tend to be cooperative, then it is possible to distinguish between cooperators and non-cooperators based on the presence of a green beard. This distinction can lead to situations where cooperators will receive the benefit of cooperation by others more often than what would be expected only by chance, potentially resulting in cooperators being better off than non-cooperators. As a matter of fact, altruistic genes associated with green beards have been discovered (Keller and Ross, 1998; Queller et al., 2003; Sinervo et al., 2006; Smukalla et al., 2008), and the evolution and maintenance of altruism can be explained by the green-beard effect. Similarly, if individuals with green beards tend to be spiteful, then it is possible to recognize spiteful individuals from non-spiteful individuals. In such a case, spiteful individuals can avoid spiteful individuals and their negative impact, so that they may end up being better off than non-spiteful individuals. In this situation too, known as Hamiltonian spite (Hamilton, 1970), genes associated with green beards have been discovered (Vassallo et al., 2017), and the evolution of spiteful behavior could be explained by the green-beard effect. In a similar way that altruism can evolve, the evolution of spite is possible as well. According to Vickery et al. (2003), spite is altruism's evil twin.

In order to measure assortative matching of individuals in a population, Bergstrom (2003, 2013) introduced the index of assortativity

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between two types i and j defined as the difference between the conditional probability that one is matched with a type i given that one is of type i and the corresponding probability given that one is of type j. This is equivalent to Wright's (1922) coefficient of relationship defined as the correlation between two individuals and used to measure relatedness in kin selection theory. It is connected to Hamilton's (1964a,b) rule for the increase in frequency of altruism in an infinite population as studied in the cases of two-pool and strangers-in-the-night assortative matching processes (Bergstrom, 2013). It can be applied to find the evolutionarily stable degree of altruism (Alger, 2003; Alger and Weibull, 2013). On the other hand, Madgwick (2020) used an assortment factor α that describes the probability for an allele in an actor to interact with a copy of itself in the case of positive assortment (or not of itself in the case of negative assortment) in a recipient over and above the expectation. Negative assortment with the possibility for recipients to interact multiple times with actors leads to a negative relatedness coefficient that is frequency dependent. The case of actors and recipients interacting only once can be dealt with by matching as many individuals as possible in mixed pairs and the remaining individuals in homogeneous pairs (Jensen and Rigos, 2018). Positive as well as negative selective assortment in pairwise interactions following a given number of encounters has been considered in the case of multiple strategies (Izquierdo et al., 2024). Mechanisms of positive assortment within groups such as the leader driven group-formation model has been studied in infinite populations using the replicator equation (Kristensen et al., 2022, 2025) as well as in finite populations with diffusion approximations (Martin and Lessard, 2023; 2024).

On the other hand, West and Gardner (2010) empirically pointed out that there is a difference in the abundance of altruistic behavior and spiteful behavior. Specifically, while altruistic behavior is abundant, spiteful behavior is rare. This suggests that negative assortment is less widespread than positive assortment. Why can there be such an asymmetry?

Several models of pairwise interactions have predicted that spite is less likely to evolve than altruism. This is the case, for instance, in a scenario where individuals can choose to repeat or not to repeat an interaction with a partner based on the partner's behavior (Kurokawa, 2024). In this scenario, costly repeated interactions with spiteful individuals can be avoided. However, this is a specific model of pairwise interactions like many others that have been analyzed up to now (see, e.g., Gardner and West, 2004, and West and Gardner, 2010).

In this paper, we consider a general model of pairwise interactions within groups of a fixed size n. We only assume that the probability distribution of the group types depends on the frequency of spite or altruism in the whole population. We analyze the evolutionary outcomes in both infinite populations, where we study instantaneous increases in frequency, and in finite populations, where we focus on fixation probabilities (Table 1).

The rest of this paper is organized as follows. In Section 2, we give an example illustrating our main argument. In Section 3, we describe the model and mathematical tools used to study of the evolution of altruistic and spiteful behaviors. In Section 4, we present our conclusions on the deterministic dynamics in infinite populations and the stochastic dynamics in finite populations, focusing on the best possible scenario for the evolution of spite compared to the best possible scenario for the evolution of altruism. In Section 5, we interpret the conditions that favor the evolution of spite and altruism in terms of some average index of assortativity, negative or positive, and explain why spite may be less widespread than altruism in natural populations.

Table 1
The payoffs to a focal individual in a group of n individuals.

strategy of the focal individual	number of individuals using strategy 1 among the $n-1$ other individuals					
	$n-1$	$n-2$	$n-3$	…	1	0
1	$-c+b$	$-c+b\frac{n-2}{n-1}$	$-c+b\frac{n-3}{n-1}$	…	$-c+b\frac{1}{n-1}$	$-c$
2	b	$b\frac{n-2}{n-1}$	$b\frac{n-3}{n-1}$	…	$b\frac{1}{n-1}$	0

2. An example illustrating our argument

To gain an intuition for why group structures favoring altruism might be more common than those favoring spite, consider the example scenarios with pairs of individuals illustrated in Fig. 1. When the population is evenly split between actors (altruistic or spiteful) and non-actors, maximum positive assortment produces all same-type pairs (Fig. 1a) and maximum negative assortment produces all opposite-type pairs (Fig. 1b). Therefore, maximum assortativity produces equally group structures most favorable to altruism and group structures most favorable to spite. However, when actors outnumber non-actors (Fig. 1c and d), positive and negative assortment have asymmetric effects on group structure. Maximum positive assortment still produces all same-type pairs (Fig. 1c); however, maximum negative assortment cannot achieve all opposite-type pairs due to the surplus of actors – some same-type pairs (actor–actor) must remain (Fig. 1d). Therefore, the maximum achievable positive assortment promotes altruism more effectively than the maximum negative assortment promotes spite. A similar asymmetry arises when non-actors outnumber actors (Fig. 1e and f). Maximum positive assortment again produces all same-type pairs (Fig. 1e), but maximum negative assortment cannot achieve all opposite-type pairs due to the surplus of non-actors – some same-type pairs (non-actor– non-actor) necessarily remain (Fig. 1f). Thus, once again, the maximum achievable positive assortment promotes altruism more effectively than the maximum negative assortment promotes spite.

Similarly, in the case of pairwise interactions within groups of size $n > 2$, the maximum positive assortment should be achieved when there are as many groups of individuals of the same type as possible. On the other hand, the scenario where the maximum negative assortment is achieved is less obvious. The main reason is that this scenario must involve groups of individuals of different types in which interactions between individuals of the same type must occur. This should make negative assortment more difficult to achieve and more so as the group size n increases.

In summary, situations of positive assortment where altruistic behavior can be favored may exist regardless of the frequency of actors, while situations of negative assortment where spiteful behavior can be favored are less common since they involve constraints on the frequency of actors. From this, it may seem that spiteful behavior is less likely to evolve than altruistic behavior.

However, all of the above is merely a verbal argument that needs to be confirmed by analytical results.

3. Materials and methods

3.1. Defining an index of assortativity

In this section, we use a minimal group-structured population model for the evolution of altruistic or spiteful behavior to derive an index of assortativity.

We consider a scenario where interactions occur in groups of n individuals, with each individual adopting either strategy 1 or strategy 2. Strategy 1 corresponds to an action which provides a payoff a to the individual who uses it and a payoff $b/(n-1)$ to each of the $n-1$ other individuals in the same group, called recipients. An individual who uses strategy 2 does nothing. Here, we assume that the payoffs are additive as in Ohtsuki (2014) and Martin and Lessard (2023). Under this assumption, the payoff to a focal individual according to its type and the number of individuals k using strategy 1 among the n individuals in its group is given by

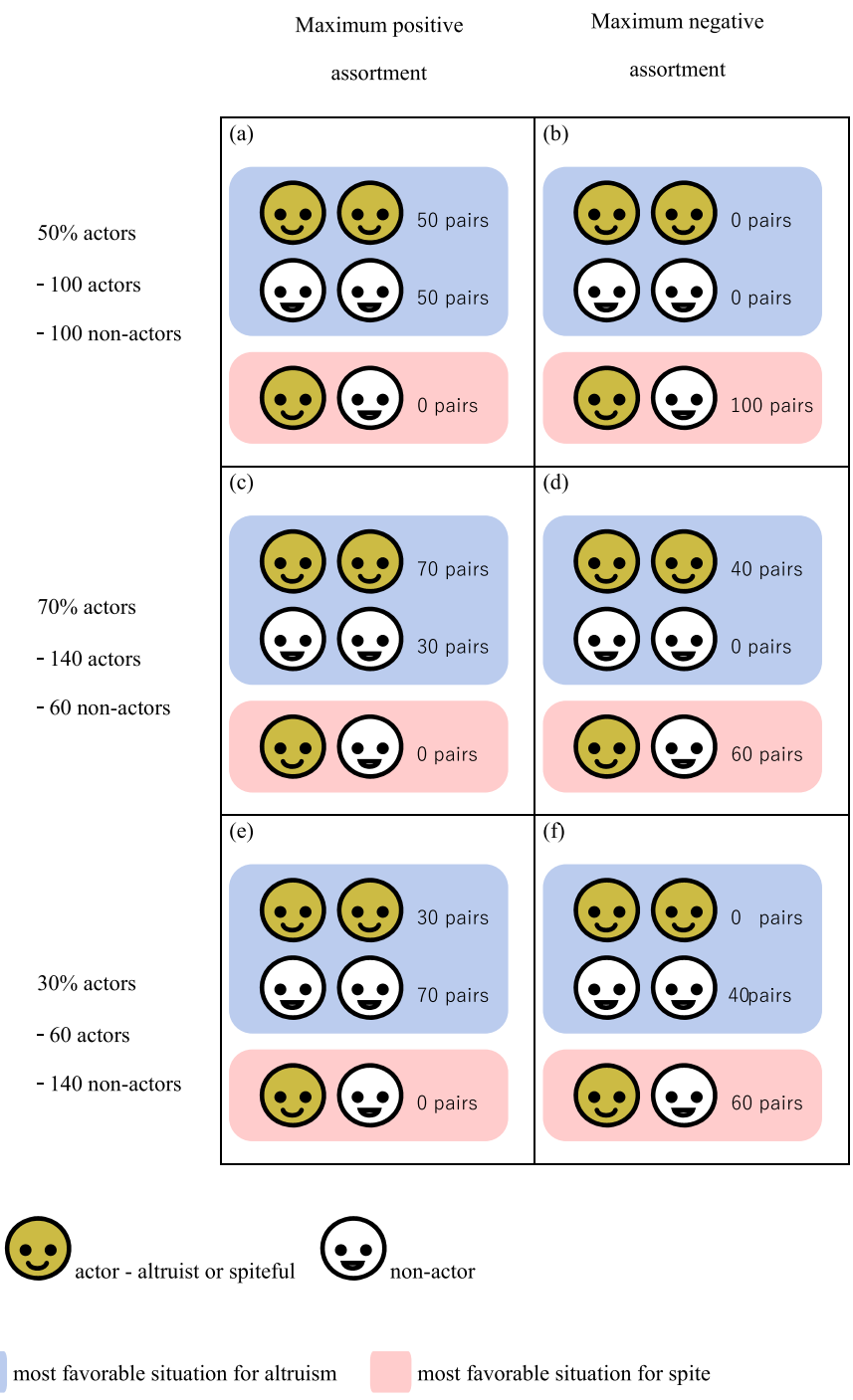

Fig. 1. Effects of population-composition on group-composition in a population of 200 individuals forming 100 pairs simultaneously. Same-type pairs (blue shading) is the most favorable situation for altruism while opposite-type pairs (rose shading) is the most favorable situation for spite. When actors (altruistic or spiteful) and non-actors are equally frequent (100 each, top row), maximum positive assortment produces 50 actor–actor pairs and 50 non-actor–non-actor pairs (a), while maximum negative assortment produces 100 actor–non-actor pairs (b). When actors outnumber non-actors (140 actors, 60 non-actors, middle row), maximum positive assortment produces 70 actor–actor pairs and 30 non-actor–non-actor pairs (c), while maximum negative assortment produces 60 actor–non-actor pairs and 40 actor–actor pairs (d). When non-actors outnumber actors (60 actors, 140 non-actors, bottom row), maximum positive assortment produces 30 actor–actor pairs and 70 non-actor–non-actor pairs (e), while maximum negative assortment produces 60 actor–non-actor pairs and 40 non-actor– non-actor pairs (f).

$$\varphi_1(k) = -c + b\frac{k-1}{n-1}$$

for an individual of type 1 for $1 \leq k \leq n$, and

$$\varphi_2(k) = b\frac{k}{n-1}$$

for an individual of type 2 for $0 \leq k \leq n-1$.

When a and b are both >0, strategy 1 is mutualistic. When a is >0 and b is <0, strategy 1 is selfish. When a is <0 and b is >0, strategy 1 is altruistic. When both a and b are <0, strategy 1 is spiteful. Evolutionary biologists are intrigued by the evolutionary origins of behaviors that incur a cost to the actor. Thus, throughout this paper, we assume $a = -c < 0$.

We denote the frequency of strategy 1 in the whole population by x. Here, we have $0 \leq x \leq 1$ and $1 - x$ is the frequency of strategy 2. Interactions occur within the groups whose size is n and we let z_k denote the frequency of groups consisting of k individuals using strategy 1 and $n - k$ individuals using strategy 2, for $0 \leq k \leq n$. These frequencies are assumed to be continuous functions of x in [0, 1]. Moreover, they must sum up to 1 and satisfy the identity

$$\sum_{k=0}^{n} \frac{k}{n} z_k = x.$$

This means that the weighted average frequency of strategy 1 in all the groups is the same as the average frequency of strategy 1 in the whole population.

Given that a focal individual chosen at random in the population uses strategy i, let $Q_{j|i}(x)$ denote the conditional probability that an individual randomly picked from among the $n-1$ other individuals in the focal individual's group uses strategy j, for $i, j = 1, 2$. Then, we have

$$Q_{1|1}(x) = \frac{\sum_{k=0}^{n} \frac{k(k-1)}{n(n-1)} z_k}{x}$$

for $0 < x \leq 1$, where the numerator on the right-hand side is the probability for both individuals to use strategy 1 obtained by conditioning on the group type. Similarly, we have

$$Q_{1|2}(x) = \frac{\sum_{k=0}^{n} \frac{k(n-k)}{n(n-1)} z_k}{1-x}$$

for $0 \leq x < 1$. Moreover, we have $Q_{1|1}(1) = 1$ and $Q_{1|2}(0) = 0$, while we define $Q_{1|1}(0) = \lim_{x \to 0} Q_{1|1}(x)$ and $Q_{1|2}(1) = \lim_{x \to 1} Q_{1|2}(x)$ under the assumption that $Q_{j|i}(x)$ for $i, j = 1, 2$ are continuous functions on [0 1].

The values of $Q_{1|1}(0)$ and $Q_{1|2}(1)$ can be determined if the group type frequencies as functions of the strategy frequencies are known. For instance, in the particular case where $z_k = \binom{n}{k} x^k (1-x)^{n-k}$ for $0 \leq k \leq n$, we have $Q_{1|1}(x) = x$ and $Q_{1|2}(x) = x$, from which $Q_{1|1}(0) = 0$ and $Q_{1|2}(1) = 1$. On the other hand, if $z_n = x$, $z_0 = 1 - x$ and $z_k = 0$ for $1 \leq k \leq n-1$, then $Q_{1|1}(x) = 1$ and $Q_{1|2}(x) = 0$, from which $Q_{1|1}(0) = 1$ and $Q_{1|2}(1) = 0$.

Now, let $\pi_i(x)$ denote the average payoff to strategy i in the population for $i = 1, 2$. Since the payoffs within groups are linear functions with respect to the number of individuals using strategy 1, the average payoff in the whole population is determined entirely by $Q_{1|1}(x)$ and $Q_{1|2}(x)$ besides b and c. No other aspects of the group structure play a role. More specifically, we have

$$\pi_1(x) = \frac{\sum_{k=0}^{n} k z_k \varphi_1(k)}{\sum_{k=0}^{n} k z_k} = -c + bQ_{1|1}(x)$$

$$\pi_2(x) = \frac{\sum_{k=0}^{n} (n-k) z_k \varphi_2(k)}{\sum_{k=0}^{n} (n-k) z_k} = bQ_{1|2}(x)$$

By using the above equations, the difference in the average payoffs is given by

$$\pi_1(x) - \pi_2(x) = -c + bR(x)$$

where

$$R(x) \equiv Q_{1|1}(x) - Q_{1|2}(x) = \frac{\sum_{k=0}^{n} \frac{k(k-1)}{n(n-1)} z_k - x^2}{x(1-x)}$$

for $0 < x < 1$, while $R(0) \equiv Q_{1|1}(0) \geq 0$ and $R(1) \equiv 1 - Q_{1|2}(1) \geq 0$. When the above difference in average payoffs yields a positive value, strategy 1 is expected to increase in frequency. In the case of altruism ($b > 0$), this requires the difference in conditional probabilities of interaction, $R(x)$, to be positive and large enough, while in the case of spite ($b < 0$), this difference must be negative and large enough in absolute value.

The difference $R(x)$ was called the index of assortativity in Bergstrom (2003). It can be shown (Bergstrom, 2013) that it is equivalent to Wright's (1922) correlation coefficient known as F-statistic. It was also noticed that $x(1 - Q_{1|1}(x)) = (1-x)Q_{1|2}(x)$ for $0 \leq x \leq 1$, since the number of individuals of type 1 interacting with an individual of type 2 must be equal to the number of individuals of type 2 interacting with an individual of type 1.

3.2. Time dynamics in an infinite population and a finite population

In an infinite population with the average payoffs as relative growth rates—thus assuming global selection so that fitness differences act across the whole population—the deterministic dynamics of the strategy frequencies follow the replicator equation (Taylor and Jonker, 1978, see Hofbauer and Sigmund, 1998, Chapter 7). It is given here by the continuous-time derivative

$$dx/dt = x(1-x)(\pi_1(x) - \pi_2(x))$$

This assumes instantaneous interactions in groups of size n whose probability distribution depends on the current strategy frequencies in the whole population and the assortment rules within groups. This determines the overall average payoffs which in turn determine the relative growth rates of the strategy frequencies as in classical evolutionary game theory.

Then the frequency x of strategy 1 increases if and only if $dx/dt > 0$. This is the case for $0 < x < 1$ if and only if $\pi_1(x) - \pi_2(x) > 0$. Assuming smooth enough average payoffs, the fixation states 0 and 1 are stable if $\pi_1(0) - \pi_2(0) < 0$ (which implies a decrease to 0 when starting close enough to 0) and $\pi_1(1) - \pi_2(1) > 0$ (which implies an increase to 1 when starting close enough to 1), respectively, while an internal equilibrium x^* is stable if the slope of $\pi_1(x) - \pi_2(x)$ at x^* is negative (which implies convergence to x^* when starting close enough to x^*). The condition $\pi_1(0) - \pi_2(0) > 0$ ensures an increase in frequency of strategy 1 when rare. This is a condition for selection to favor the evolution of strategy 1 in an infinite population.

In the case of a finite population where random drift takes place, the population size, denoted by N, is supposed to be finite but large. Moreover, we assume a diffusion approximation for the stochastic dynamics with infinitesimal mean

$$m(x) = sx(1-x)(\pi_1(x) - \pi_2(x))$$

and infinitesimal variance $v(x) = x(1-x)$. Here, the average payoffs correspond to differences in reproductive success, or fitness, and they are weighted by some intensity of selection $s > 0$. Such an approximation holds for a wide range of updating rules from one time step to the next in finite populations with an appropriate scaling of time in number of time steps as the population size goes to infinity. These include the Moran model with one individual replaced at a time and the Wright-Fisher model with replacement of all individuals at every time step

according to a binomial scheme. More generally, it holds for a wide class of exchangeable selection models with the numbers of descendants of individuals using the same strategy from one time step to the next being exchangeable random variables (see Martin and Lessard, 2023, and references therein).

Owing to diffusion theory (see, e.g., Ewens, 2004, Section 4), the fixation probability of strategy 1 from any initial frequency in a population of large finite size N can be calculated. When strategy 1 is introduced as a single mutant in a population that was fixed for strategy 2, its initial frequency is $1/N$ and its fixation probability is approximated by

$$\rho_1 \approx \frac{\int_0^{1/N} \psi(y)dy}{\int_0^1 \psi(y)dy}$$

where

$$\psi(y) = e^{-2\int_0^y \frac{m(x)}{v(x)}dx} = e^{-2s\int_0^y (\pi_1(x)-\pi_2(x))dx}$$

for $0 \le y \le 1$. Then selection is said to favor strategy 1 replacing strategy 2 when $\rho_1 > 1/N$, where $1/N$ is the fixation probability in the absence of selection (Nowak et al., 2004). Similarly, selection is said to disfavor strategy 2 replacing strategy 1 when $\rho_2 < 1/N$, where ρ_2 is the fixation probability of strategy 2 starting from an initial frequency $1\ /N$. These are two conditions for selection to favor the evolution of strategy 1 over strategy 2 in a finite population.

It is known that the evolution of a strategy can be favored by selection in a finite population under the effect of random drift even if this strategy cannot initially invade an infinite population. Moreover, two competing strategies, 1 and 2, can be favored by selection to replace each other in a population of finite size N in the sense that their fixation probabilities when introduced as single mutants denoted by ρ_1 and ρ_2 satisfy $\rho_1 > 1/N$ and $\rho_2 > 1/N$. Strategy 1 is more likely to replace strategy 2 than vice versa when $\rho_1 > \rho_2$. This is another condition for selection to favor the evolution of strategy 1 over strategy 2 in a finite population (Nowak et al., 2004).

4. Results

4.1. Range of values for the index of assortativity

We begin by establishing the bounds of the index of assortativity $R(x)$. First, we find that $R(x)$ reaches its maximum value of 1 under complete segregation, where all groups contain only individuals of the same type. We define $z_k{}^*$ for $0 \le k \le n$ as the values of z_k for $0 \le k \le n$ that maximize $R(x)$. From this definition, we can draw the following conclusion (see Appendix A in SM): $z_k{}^* = 0$ for $1 \le k \le n-1$. Substitution of these values into the constraints on the group frequencies yields $z_n{}^* = x$ and $z_0{}^* = 1-x$, from which

$$R(x) \le \frac{\sum_{k=0}^{n} \frac{k(k-1)}{n(n-1)} z_k{}^* - x^2}{x(1-x)} = 1 \equiv r_n{}^*(x).$$

This upper bound 1 for the index of assortativity $R(x)$ is not surprising since it is a difference of two probabilities. What is interesting is that this upper bound is achieved in the case of complete segregation with all groups containing only individuals of the same type (Jensen and Rigos, 2018).

Having established the upper bound of $R(x)$, we now turn our attention to the lower bound. By symmetry with the upper bound 1, one might expect the lower bound to be -1, but we find that the index of assortativity is constrained to a smaller magnitude when minimized. We define $z_k{}^{**}$ for $0 \le k \le n$ as the values of z_k for $0 \le k \le n$ that minimize $R(x)$. From this definition, we have the following identity (see Appendix B in SM): $z_k{}^{**} = 0$ for $k \le j-1$ and $k \ge j+2$ if $j \le nx < j+1$ for $0 \le j \le n-1$. Then, we have $j = \lfloor nx \rfloor$, which represents the integer value of nx and the constraints on the group frequencies yield $z_{j+1}{}^{**} = nx - j$ and $z_j{}^{**} = j + 1 - nx$. An important intuition derived from this result is that the index of assortativity is minimized when group compositions are as evenly mixed as possible. Ideally, each group would contain exactly nx individuals playing strategy 1, where n is the group size and x is the overall frequency of strategy 1 in the population. However, since group sizes must be integers and nx is generally not an integer, the optimal configuration involves a mixture of two group types: one with $j = \lfloor nx \rfloor$ individuals using strategy 1, and another with $j+1$. The values of $z_k{}^{**}$ lead to

$$R(x) \ge \frac{\sum_{k=0}^{n} \frac{k(k-1)}{n(n-1)} z_k{}^{**} - x^2}{x(1-x)} = \frac{\lfloor nx \rfloor}{n(n-1)} \frac{2nx - (\lfloor nx \rfloor + 1)}{x(1-x)} - \frac{x}{(1-x)} \equiv r_n{}^{**}(x).$$

This gives the lower bound $r_n{}^{**}(x)$ for $R(x)$.

It can also be shown (see Appendix B in SM) that for any x satisfying $0 < x < 1$, we have

$$r_n{}^{**}(x) \ge -\frac{1}{n-1}$$

with an equality if and only if nx is an integer.

In summary, we have the inequalities

$$-\frac{1}{n-1} \le r_n{}^{**}(x) \le R(x) \le r_n{}^{*}(x) = 1$$

Most importantly, the magnitude of the lower bound is less than or equal to the magnitude of the upper bound, that is, $|r_n{}^{**}(x)| \le |r_n{}^{*}(x)|$. The equality holds if and only if $n = 2$ and $x = 1/2$. Moreover, the lower bound $r_n{}^{**}(x)$ depends on x while the upper bound $r_n{}^{*}(x)$ does not. Specifically, from the above expression for $r_n{}^{**}(x)$, one can show that $r_n{}^{**}(x) = r_n{}^{**}(1-x)$, and $r_n{}^{**}(x)$ tends to zero as the frequency x tends 0 or 1.

Fig. 2 illustrates the range of values for $R(x)$. This allows us to visualize the statements just made.

4.2. Evolutionary dynamics of spite and altruism in an infinite population

The dynamics of the strategy frequencies in an infinite population is given by the replicator equation

$$dx/dt = x(1-x)(-c + bR(x)),$$

derived from $\pi_1(x) - \pi_2(x) = -c + bR(x)$ and $dx/dt = x(1-x)(\pi_1(x) - \pi_2(x))$. Owing to the inequalities in the summary of the previous subsection, the condition $-c + bR(x) > 0$ gives more room for an increase in frequency of altruism ($b > 0$), which requires a positive value of $R(x)$ large enough, than for an increase in frequency of spite ($b < 0$), which requires a negative value large enough in absolute value.

Moreover, as pointed out in the previous subsection, the value of the lower bound $r_n{}^{**}(x)$ of $R(x)$ is close to zero when x is close to zero. Besides, we already know that $R(0) \ge 0$. Therefore, spite introduced in small frequency is generally unable to invade the population, while this is still possible for altruism. The evolution of spite is therefore more difficult to explain than the evolution of altruism. This is consistent with a well-known prediction (Hamilton, 1964a, 1964b, 1971).

Finally, if $-c + bR(0) < 0$, which implies that $x = 0$ is stable, then the internal equilibrium with the smallest frequency of spite or altruism denoted by $x_0 > 0$, when it exists, is unstable since the slope of $-c + bR(x)$ at $x = x_0$ cannot be negative. This represents a threshold for the frequency of spite or altruism to increase.

4.3. Evolutionary dynamics of spite in a finite population

A diffusion approximation for the frequency of strategy 1 (spite or altruism) in competition with an alternative strategy 2 in a large finite

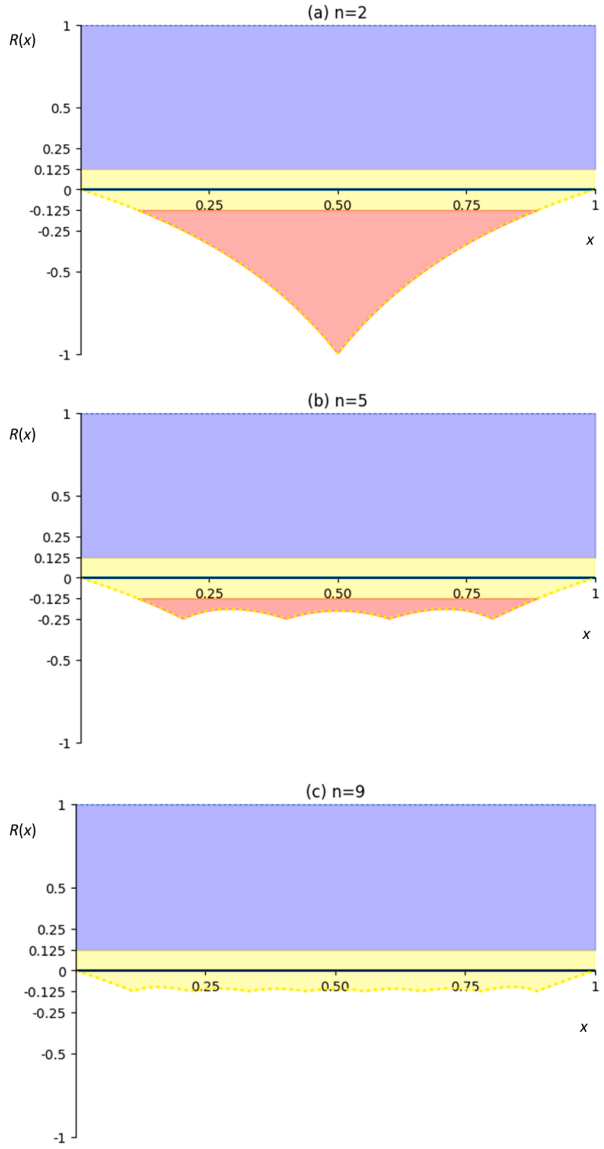

Fig. 2. Range of values of the index of assortativity $R(x)$ as a function of x. In blue is the region where altruistic individuals have a higher average payoff than non-altruistic individuals ($R(x) > c/b$ for $c = 1$ and $b = 8$) and in rose the region where spiteful individuals have a higher average payoff than non-spiteful individuals ($R(x) < c/b$ for $c = 1$ and $b = -8$), while the region where neither of these events occurs is in yellow, for three group sizes: (a) $n = 2$, (b) $n = 5$, and (c) $n = 9$.

population has infinitesimal variance $v(x) = x\,(1-x)$ and infinitesimal mean

$$m(x) = sx(1-x)(-c+bR(x)),$$

derived from $\pi_1(x) - \pi_2(x) = -c + bR(x)$ and $m(x) = sx(1-x)(\pi_1(x) - \pi_2(x))$, for some intensity of selection $s > 0$.

Let ρ_1 and ρ_2 denote the probabilities for strategies 1 and 2, respectively, introduced as single mutants to fix in a population of size N. The following equivalences hold for N large enough and s small enough (see Appendix C in SM):

$$\rho_1 > 1/N \text{ if and only if } -c + b\int_0^1 2(1-x)R(x)dx > 0,$$

$$\rho_2 < 1/N \text{ if and only if } -c + b\int_0^1 2xR(x)dx > 0,$$

$$\rho_1 > \rho_2 \text{ if and only if } -c + b\int_0^1 R(x)dx > 0.$$

The three necessary and sufficient conditions above are in the form $-c + b\overline{R} > 0$, where $\overline{R}$ is an average of the index of assortativity $R(x)$ with respect to the density function $2(1-x)$, $2x$ and 1 for $0 \le x \le 1$, respectively.

In the previous subsection, we considered the deterministic model for an infinite population and showed that it cannot explain the evolution of spite since its initial increase in frequency is generally not possible. Here, we examine the situation where spite is most likely to evolve in a finite population. This is the case when $R(x) = r_n^{**}(x)$ holds true. Under this condition, the fixation probability of spite introduced as a single mutant into a population composed entirely of non-spiteful individuals, represented by ρ_1, exceed its initial frequency, $1/N$, if and only if

$$-c + b\overline{r_n^{**}} > 0$$

where $b < 0$ and

$$\overline{r_n^{**}} \equiv \int_0^1 2(1-x)r_n^{**}(x)dx.$$

Moreover, by using the exact expression of $r_n^{**}(x)$ (see Appendix C in SM), we obtain the formula

$$\overline{r_n^{**}} = 1 + \frac{4}{n(n-1)}\sum_{k=1}^{n-1} k\log\frac{k}{n}.$$

Similarly, the condition under which the fixation probability of the non-spiteful strategy, represented by ρ_2, is smaller than $1/N$ when a single non-spiteful individual is introduced into a population composed entirely of spiteful individuals is $-c + b\overline{r_n^{**}} > 0$. This is the case since the identity $r_n^{**}(x) = r_n^{**}(1-x)$ implies

$$\overline{r_n^{**}} = \int_0^1 2(1-x)r_n^{**}(1-x)dx = \int_0^1 2xr_n^{**}(x)dx.$$

Moreover, the condition to have $\rho_1 > \rho_2$ is also given by $-c + b\overline{r_n^{**}} > 0$, since

$$\overline{r_n^{**}} = \int_0^1 (1-x)r_n^{**}(x)dx + \int_0^1 xr_n^{**}(x)dx = \int_0^1 r_n^{**}(x)dx$$

owing to the previous expressions of $\overline{r_n^{**}}$. Therefore, the above three conditions favoring the evolution of spite reduce to the same condition.

From the above definitions (see Appendix D in SM), it can be shown that

$$-1 < \overline{r_n^{**}} < \overline{r_{n+1}^{**}} < 0$$

for $n \ge 2$ with $\overline{r_2^{**}} = 1 - 2\log 2$. This implies that, as n increases, the evolution of spite becomes more difficult (see Fig. 3).

Furthermore, for n large enough (see Appendix C in SM), we have the approximation

$$\overline{r_n^{**}} \approx -\frac{1}{n-1} + \frac{3 + 2\log(2n)}{4n(n-1)},$$

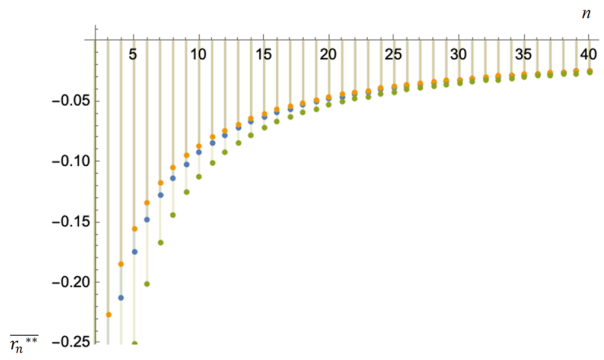

Fig. 3. Relationship between the lower bound $\overline{r_n^{**}}$ and the group size n. Here, $\overline{r_n^{**}}$ (yellow dot) represents the minimum value of the ratio c/b for selection to favor the evolution of spite in a finite population, bounded below by $-\frac{1}{n-1}$ (green dot) and approached by $-\frac{1}{n-1}+\frac{3+2\log(2n)}{4n(n-1)}$ (blue dot) for n large enough.

which increases to 0 as n goes to infinity.

4.4. Evolutionary dynamics of altruism in a finite population

Now, we consider the case where altruism is most likely to evolve in a finite population, that is, $R(x) = 1$. In this case, the conditions for $\rho_1 > 1/N$, $\rho_2 < 1/N$, $\rho_1 > \rho_2$ all reduce to the inequality

$$-c + b > 0,$$

where $b > 0$. Notice that this condition does not depend on the group size n. Moreover, this condition for the evolution of altruism is less stringent than the condition for the evolution of spite for b having the same absolute value, the discrepancy increasing as the group size n increases.

5. Discussion

Altruistic behavior is more common in nature than spiteful behavior (West and Gardner 2010). In this paper, we have used a general mathematical framework to show that there is more room for the evolution of altruism than for the evolution of spite. Assuming pairwise interactions with additive effects on payoff in groups of fixed size n, but any probability distribution for the group composition that depends only on the frequency of spite or altruism in the whole population, represented by x, we have deduced evolutionary properties based on the index of assortativity $R(x)$ (Bergstrom, 2003, 2013). We have shown that the range of positive values of $R(x)$ for selection to favor the evolution of altruism is much larger than the range of negative values of $R(x)$ for selection to favor the evolution of spite. Specifically, $R(x)$ has a positive upper bound of $r_n^*(x) = 1$ associated with as many same-type pairs as possible within groups, but a negative lower bound of $r_n^{**}(x) \geq -1$ associated with the maximum number of opposite-type pairs, which tends to 0 as x tends to 0 or 1. This asymmetry is particularly important for explaining a major difference between evolutionary properties of altruism and spite in an infinite population: altruistic behavior can invade the population from low initial frequencies, whereas spiteful behavior generally cannot. In a finite population, the conditions for selection to favor spite or altruism based on fixation probabilities depend on an average $\overline{R}$ for the index of assortativity $R(x)$. This average satisfies $\overline{r_n^{**}} \leq \overline{R} \leq \overline{r_n^*}$, where the upper bound is constant and given by $\overline{r_n^*} = 1$, while the lower bound $\overline{r_n^{**}}$ is negative and increases from $1 - 2\log 2$ to 0 as the group size n increases from 2 to infinity. This makes the interval of negative values of $\overline{R}$ for selection to favor the fixation of spite, $[\overline{r_n^{**}}, 0]$, shorter than the interval of positive values for selection to favor the fixation of altruism, $[0, \overline{r_n^*}]$, and more so as for larger n.

Previous work comparing the evolution of spite to the evolution of altruism has focused on specific models. In a model where individuals can choose to either continue or terminate an interaction with a partner based on the partner's behavior or the composition of the group, Kurokawa (2023, 2024) showed that the evolution of spite in an infinite population may be facilitated even though the evolution of spite remains less likely than the evolution of altruism (see also Kurokawa (2021)). In a model consisting of M subpopulations, each comprising N individuals and with updating according to a two-level Moran process, Kurokawa and Ihara (2013) found that, as M varied from 1 to infinity, a dyadic kinship-like measure $(M-2)/(M+N-2)$ increased from $-1/(N-1)$ to 1 as M increased. Their conclusion was similar to the one reached in this paper: because the range of positive-assortment values possible was larger than the range of negative-assortment values, the group structures that promote the evolution of altruism are more numerous than the structures that promote spite. On the other hand, Lehmann et al. (2009) modelled the coevolution of neutral recognition markers and marker-based conditional altruistic or spiteful behavior. They highlighted conditions where the selective pressure for conditional harming was stronger than for conditional helping in the context of competition for limited resources in both finite panmictic and infinite structured populations. These are conditions where spiteful behavior is more likely to evolve than altruistic behavior, but conditions for the opposite can still be more widespread in natural populations.

In contrast to previous works, we have not made any assumption on how groups are formed or how the population is updated from one time step to the next. Moreover, we have not examined precise conditions for the evolution of altruistic and spiteful behaviors, but rather the spectrum of possibilities for their evolution in group-structured populations. These have been obtained by considering the best possible scenarios for their initial increase in frequency in an infinite population or their ultimate fixation after being introduced as a single mutant in a finite population. Our findings indicate not only that spiteful behavior cannot generally increase in frequency when rare in an infinite population contrary to altruistic behavior, but that spiteful behavior is less likely to evolve than altruistic behavior in a large finite population based on comparisons of fixation probabilities when introduced as single mutants. Moreover, this holds true not only for groups of any fixed size n but is enhanced as n increases. This might explain why spiteful behavior is less common in nature compared to altruistic behavior.

Kurokawa (2023) considered an n-player game where the interactions between the individuals chosen at random could either continue or terminate based on the behaviors of the n individuals. The conditions for the evolution of spiteful behavior in that model are more stringent than those derived in the present paper in which we have considered the most favorable assortment within groups for such an evolution. This is actually the case for every model that falls within the scope of our general framework.

In a context of pairwise interactions in an infinite population, Madgwick (2020) introduced the concept of a constant assortment factor α defined as the probability for an actor to interact with a recipient of the same type (for positive assortment) or a recipient of a different type (for negative assortment) over and above the random expectation. In the case of discriminate spite (i.e., only non-spiteful partners are affected) or indiscriminate spite (i.e., all partners are affected) with one-way assortment (spiteful individuals interacting once, non-spiteful individuals any number of times), the condition for the increase in frequency of spite with current frequency x is given by Hamilton's rule $-c + br(x) > 0$ (Hamilton, 1964a, 1964b) with negative frequency-dependent coefficient of relatedness $r(x) = -\alpha x/(1-x)$ (see also Hamilton, 1970, 1971, Grafen, 1985 and Patel et al., 2020, about the concept of negative relatedness). For comparison, Hamilton's rule for the increase in frequency of altruism with positive assortment holds with coefficient of relatedness $r(x) = \alpha$.

We have shown that Hamilton's rule for the increase in frequency of

indiscriminate spite or altruism in an infinite population with pairwise interactions in groups of any fixed size n having any probability distribution holds with frequency-dependent coefficient of relatedness given by the index of assortativity $R(x)$ as defined in Bergstrom (2003, 2013). Furthermore, the condition for selection to favor the fixation of spite or altruism introduced as a single mutant in a finite population is given by Hamilton's rule with coefficient of relatedness $\overline{R}$ that is an average of $R(x)$ with respect to the density function $f(x) = 2(1-x)$ for $0 \leq x \leq 1$. This is the density function for the fraction of mean effective sojourn time for the frequency of spite or altruism from its introduction as a single mutant up to its fixation or extinction in a neutral population with all zero payoffs (Ohtsuki et al., 2007, Martin and Lessard, 2024). By symmetry, the condition for selection to favor the extinction of spite or altruism in a population invaded by a single non-spiteful or non-altruistic individual involves a coefficient of relatedness $\overline{R}$ that is the integral of $R(x)$ with respect to the density function $g(x) = 2x$ for $0 \leq x \leq 1$. Furthermore, selection favors more the fixation of spite or altruism than its extinction when $-c + b\overline{R} > 0$, where $\overline{R}$ is the integral of $R(x)$ with respect to the density function $h(x) = (f(x) + g(x))/2 = 1$ for $0 \leq x \leq 1$. This is also the condition for spite or altruism to be more abundant on average than the alternative strategy in the stationary state of a population under recurrent mutation in the limit of a low mutation rate (Fudenberg and Imhof, 2006; Fudenberg et al., 2006; Lessard, 2025). In this context, the fraction of mean effective sojourn time for the frequency of spite or altruism in the long run in a neutral population has a density function given by $h(x) = 1$ for $0 \leq x \leq 1$. Finally, in the best scenarios for the evolution of altruism ($R(x) = \overline{r_n^*}(x)$ for $0 \leq x \leq 1$) and the evolution of spite ($R(x) = \overline{r_n^{**}}(x)$ for $0 \leq x \leq 1$), the integrals of $R(x)$ with respect to the density functions $f(x)$, $g(x)$ and $h(x)$ for $0 \leq x \leq 1$ are the same.

It is worth mentioning that while we have considered dyadic interactions within groups, Madgwick (2020) focused on dyadic interactions in the whole population. On the other hand, he considered not only discriminate spite, which requires some kind of recognition, besides indiscriminate spite but also cases where actors (spiteful or altruistic individuals) may interact only once besides cases where they may interact several times. This allows for more flexible patterns of pair formation (see also Jensen and Rigos, 2018, for extensions to n-player games). This is not the case in the present paper, where spite or altruism is always indiscriminate and all individuals can interact several times. However, it is likely that similar conclusions can be drawn under more relaxed assumptions.

Some particular mechanisms of positive selective assortment in social dilemmas such as assortment by group founders, also called leader-driven assortment, were recently analyzed in more detail (Kristensen et al., 2022, 2025; Martin and Lessard, 2023; 2024). This kind of assortment is actually easier to study than structural assortment associated with mating constraints as occurs in island models with partial dispersal (Rousset, 2004; Lehman and Rousset, 2010; Ohtsuki, 2010; Lessard, 2011a,b), which makes appeal to two-timescale arguments (Lessard, 2025). The conclusions, however, are similar. Mechanisms of negative selective assortment raises further challenges and deserves more attention.

Our results have been obtained under the assumption of global selection. In the case of local selection with equal contributions of groups (Hilbe, 2011), a measure of tripletwise assortment besides the index of assortativity $R(x)$ for pairwise assortment may come into play (see, e.g., Martin and Lessard, 2023). For the model at hand, it can be checked directly (see Appendix E in SM) that the rate of change in the frequency of spite or altruism under local selection—acting within subpopulations or demes and shaped by local competition and ecological constraints—in an infinite population is given by

$$\begin{aligned}\frac{dx}{dt} &= \sum_{k=0}^{n} \frac{k}{n}\left(1-\frac{k}{n}\right)(\varphi_1(k)-\varphi_2(k)) \\ &= \frac{n-1}{n}\left(-c-\frac{b}{n-1}\right)x(1-x)(1-R(x)).\end{aligned}$$

This is also the infinitesimal mean of the diffusion approximation for the stochastic dynamics in a finite population up to a positive multiplicative factor representing the intensity of selection. Therefore, the condition for an increase in frequency of spite or altruism in an infinite population is $-c - b/(n-1) > 0$ unless $R(x) = 1$. This is also the condition for selection to favor spite or altruism in a finite population based on fixation probabilities unless the integrals of $(1-R(x))$ with respect to the density functions $f(x)$, $g(x)$ and $h(x)$ for $0 \leq x \leq 1$ are equal to 0 (see Appendix E in SM). This is the case if and only if $R(x) = 1$ for $0 \leq x \leq 1$. This conclusion agrees with results for the evolution of altruism obtained in Lehman and Rousset (2010) and Martin and Lessard (2023) with particular mechanisms of positive assortment. What is important to point out here is that while this condition cannot hold for altruism ($c > 0$ and $b > 0$), it may hold for spite ($c > 0$ and $b < 0$) when the group size n is not too large. Contrary to altruism, spite is more likely to evolve under local selection than under global selection.

We will now outline some limitations of our study. Firstly, our analysis has focused on two extreme scenarios for the evolution of spite and the evolution of altruism. It is important to note that these scenarios will generally not be met in practice. Therefore, the real conditions for the evolution of these behaviors could be more stringent than what these scenarios suggest. Secondly, the model presented in this paper does not encompass all possible strategies. Our model does not allow for players to exhibit moderate levels of altruism or spite, nor does it accommodate behavioral switches in response to different situations in repeated interactions. As a result, direct reciprocity and indirect reciprocity are beyond the scope of this study (see, e.g., Fletcher and Doebeli, 2009).

Finally, we have examined conditions favoring the evolution of altruism or spite without specifying any mechanism of assortment, yielding a provisional result that spiteful behavior is less likely to evolve than altruism under global selection. However, both altruism and spitefulness should be driven by specific mechanisms that will determine the average payoffs and the index of assortativity $R(x)$ if the game is linear, not to mention the complexity of non-linear n-player games and more general measures of assortment. Therefore, research aimed at examining which behavior is more likely to evolve, altruism or spite, by considering a wide range of assumptions needs to be continued in the near future.

CRediT authorship contribution statement

Shun Kurokawa: Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Sabin Lessard:** Writing – review & editing, Methodology, Investigation, Formal analysis.

Declaration of competing interest

The authors declare that they have no real or apparent conflict of interest.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tpb.2025.11.001.

Data availability

No data was used for the research described in the article.

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