Evolution of cooperation in a multidimensional phenotype space

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ABSTRACT

The emergence of cooperation in populations of selfish individuals is a fascinating topic that has inspired much theoretical work. An important model to study cooperation is the phenotypic model, where individuals are characterized by phenotypic properties that are visible to others. The phenotype of an individual can be represented for instance by a vector $\mathbf{x} = (x_1, \ldots, x_n)$, where $x_1, \ldots, x_n$ are integers. The population can be well mixed in the sense that everyone is equally likely to interact with everyone else, but the behavioral strategies of the individuals can depend on their distance in the phenotype space. A cooperator can choose to help other individuals exhibiting the same phenotype and defects otherwise. Cooperation is said to be favored by selection if it is more abundant than defection in the stationary state. This means that the average frequency of cooperators in the stationary state strictly exceeds 1/2. Antal et al. (2009c) found conditions that ensure that cooperation is more abundant than defection in a one-dimensional (i.e. $n = 1$) and an infinite-dimensional (i.e. $n = \infty$) phenotype space in the case of the Prisoner's Dilemma under weak selection. However, reality lies between these two limit cases. In this paper, we derive the corresponding condition in the case of a phenotype space of any finite dimension. This is done by applying a perturbation method to study a mutation-selection equilibrium under weak selection. This condition is obtained in the limit of a large population size by using the ancestral process. The best scenario for cooperation to be more likely to evolve is found to be a high population-scaled phenotype mutation rate, a low population-scaled strategy mutation rate and a high phenotype space dimension. The biological intuition is that a high population-scaled phenotype mutation rate reduces the quantity of interactions between cooperators and defectors, while a high population-scaled strategy mutation rate introduces newly mutated defectors that invade groups of cooperators. Finally it is easier for cooperation to evolve in a phenotype space of higher dimension because it becomes more difficult for a defector to migrate to a group of cooperators. The difference is significant from $n = 1$ to $n = 2$ and from $n = 2$ to $n = 3$, but becomes small as soon as $n \geq 3$.

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1. Introduction

Evolutionary game theory is the study of frequency-dependent selection (Maynard Smith, 1982; Maynard Smith and Price, 1973; Hofbauer and Sigmund, 1988, 2003; Cressman, 2003; Nowak and Sigmund, 2004; Nowak, 2006). The fitness of an individual is not constant, since it depends on the payoff of the strategy used by the individual in interaction with other individuals. It was originally expressed in terms of the replicator equation in the case of pairwise interactions in an infinite well-mixed population, which means that any two individuals interact with the same probability (Taylor and Jonker, 1978; Hofbauer et al., 1979; Zeeman, 1980).

Consider an evolutionary game with n possible strategies, labeled by the integers $i = 1, \ldots, n$. The payoff matrix $A = (a_{i,j})$ is a $n \times n$ matrix, whose entry $a_{i,j}$ represents the payoff received by an individual playing strategy i against an individual playing strategy j. The frequency of strategy i is denoted by x_i. Then the replicator equation is given by

$$\dot{x}_i = x_i \Big(w_i(\mathbf{x}) - \overline{w}(\mathbf{x}) \Big),$$

where $w_i(\mathbf{x})$ and $\overline{w}(\mathbf{x})$ represent the expected payoff to strategy i and the average payoff in the population, respectively, given by

$$w_i(\mathbf{x}) = \sum_{j=1}^{N} a_{i,j} x_j$$

and

$$\overline{w}(\mathbf{x}) = \sum_{i=1}^{N} x_i w_i(\mathbf{x}),$$

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with $\mathbf{x} = (x_1, \ldots, x_n)$. This fundamental equation can be extended to spatial games in a graph-structured population, with every individual occupying a vertex of the graph interacting with its nearest neighbors (Ohtsuki and Nowak, 2006b), or in a group-structured population with groups of interacting individuals randomly chosen in an infinite population (Hilbe, 2011). It can be extended also to games with multiple players in a finite or infinite well-mixed population (Gokhale and Traulsen, 2010).

Infinitely large, well-mixed populations and deterministic dynamics are idealizations. Real populations have a finite number of individuals besides being not perfectly mixed. Linear games have been considered in the context of finite populations. In the absence of mutation, selection can favor or oppose a mutant strategy to replace a resident strategy. This will be the case for instance if the probability of fixation of the mutant is larger or smaller than it would be under neutrality (Rousset and Billiard, 2000; Nowak et al., 2004; Taylor et al., 2004; Lessard, 2005; Imhof and Nowak, 2006; Ladret and Lessard, 2007, 2008). In the presence of symmetric mutation, selection is said to favor a strategy if this strategy is more abundant on average, that is, if its average frequency in the stationary state strictly exceeds what it would be under neutrality (Fudenberg and Imhof, 2006; Antal et al., 2009a,b; Tarnita et al., 2009, 2011; Gokhale and Traulsen, 2011; Kroumi and Lessard, 2014).

Spatial structures have been considered more recently for games in finite populations. The spatial distribution of a population allows interactions between individuals to depend on their locations. In the traditional setting of spatial games, the individuals are arranged on a regular lattice and interactions occur among nearest neighbors (Nowak and May, 1992). A generalization of this structure is the graph structure where individuals occupy the vertices of a graph and the edges indicate who interacts with whom (Lieberman et al., 2005; Ohtsuki and Nowak, 2006a,b; Ohtsuki et al., 2006; Taylor et al., 2007a,b; Santos et al., 2008).

Another spatial structure is a population subdivided into two subpopulations with any migration rates (Ladret and Lessard, 2007), or an island model with a large number of islands and uniform or proportional dispersal (Rousset and Billiard, 2000; Ladret and Lessard, 2008; Lessard, 2011a,b). The stepping stone model (see, e.g., Rousset and Billiard, 2000; Rousset, 2006) is a spatial model with local dispersal. Suppose a population subdivided into d demes labeled by the integers $1, \ldots, d$, and a migration matrix $M = (m_{i,j})$, where $m_{i,j}$ is the proportion of offspring in deme i that come from deme j. The stepping stone model corresponds to the case where $m_{i,j} = \frac{m}{2}$ if $j = i+1$ or $i-1$, and 0 otherwise, for $i = 2, \ldots, d-1$. For $i = 1$, we have $m_{1,j} = \frac{m}{2}$ if $j = 2$ or d, and 0 otherwise. Similarly, we have $m_{d,j} = \frac{m}{2}$ if $j = 1$ or $d-1$, and 0 otherwise.

The geometry of human populations is determined by associations that individuals have with various groups or sets. Each individual may belong to many sets, for example, a student may study several subjects and take different classes. A particular setting is studied in Tarnita et al. (2009): a population of N individuals is distributed over M sets where each individual belongs exactly to K sets. Interactions occur within each given set. For a review of evolutionary dynamics in structured populations, see, e.g., Lehmann and Rousset (2010, 2014) or Nowak et al. (2010).

The Prisoner's Dilemma (Axelrod and Hamilton, 1981; Axelrod, 1984) is a simple game in which there is a tension between individual interests and a common good. It has been studied in economics, philosophy and machine learning. It is crucial for understanding human relations, evolution and morality. In the Prisoner's Dilemma, there are two strategies, C and D, which refer to cooperation and defection, respectively. The payoff matrix is given by

$$
\begin{array}{cc}
 & \begin{array}{cc} C & D \end{array} \\
\begin{array}{c} C \\ D \end{array} & \left(\begin{array}{cc} R & S \\ T & P \end{array} \right),
\end{array} \tag{1}
$$

where $T > R > P > S$. Here, R is the *reward payoff* that each player receives if both cooperate, P is the *punishment payoff* that each player receives if both defect, T is the *temptation payoff* that a player receives if he alone defects and S is the *sucker payoff* that a player receives if he alone cooperates. A simpler form of the Prisoner's Dilemma is the additive model with a payoff matrix in the form

$$
\begin{array}{cc}
 & \begin{array}{cc} C & D \end{array} \\
\begin{array}{c} C \\ D \end{array} & \left(\begin{array}{cc} b-c & -c \\ b & 0 \end{array} \right),
\end{array} \tag{2}
$$

where $b > 0$ is the benefit gained by the opponent of a cooperator and $c > 0$ is the cost incurred by a cooperator.

Individuals exhibit other phenotypic traits in addition to their behavioral strategies as size, height, or other aspects of physical appearance, which supports the idea that behavioral strategy is triggered by phenotypic similarity. This is known as the green-beard effect which is based on the theory of the selfish gene (Hamilton, 1964a,b; Dawkins, 1976), according to which an individual possesses the gene that creates the incentive to be altruistic toward individuals who also possess this gene. It appears when a gene produces three phenotypic effects: a perceptible characteristic (the hypothetical green beard), a recognition by other individuals of this characteristic and a preferential treatment of those recognized. An individual carrier of this gene recognizes the other porters of this gene and behaves in a way altruistic toward them.

The effect of phenotypic similarity on the evolution of cooperation has been studied in the framework of an infinite structured population (see, e.g., Riolo et al., 2001; Axelrod et al., 2004; Traulsen and Claussen, 2004; Jansen and Van Baalen, 2006; Traulsen and Nowak, 2007). Rousset and Roze (2007) and Lehmann et al. (2009) consider an island model with an infinite number of demes composed of N haploid individuals. There are two loci with two alleles segregating at each locus. The first is the helping locus with a helping allele or a cheating allele. The second is the matching locus with a mutant recognition allele or a wild allele. There are pairwise interactions within demes. An individual i adopts the strategy *cooperation* against an individual j of the same deme if i has the helping allele at the helping locus while i and j have the same allele at the matching locus, otherwise i adopts the strategy *defection* against j.

More recently Lehmann et al. (2009) considered a finite well-mixed population according to a Wright–Fisher model. Like in Rousset and Roze (2007), there are two loci, a strategy locus and a matching locus. With two alleles at the matching locus, a wild type and a mutant type, it is a model with a finite phenotype space, actually two phenotypes.

Another setting is the one-dimensional or infinite-dimensional phenotype space with *a priori* infinite possible states which was studied by Antal et al. (2009c). Consider a population of N individuals which follows a Wright–Fisher model. In each generation, every individual produces the same large number of offspring. The next generation of N individuals is sampled from this pool of offspring. Consider a one-dimensional (respectively infinite-dimensional) phenotype space: each individual has a phenotype represented by an integer (respectively an infinite vector of integers) and adopts a strategy among the two strategies of the Prisoner's Dilemma, C and D. An individual inherits its parent's phenotype i with probability $1 - v$, or one of the phenotypes $i - 1$ and $i + 1$ with the same probability $v/2$ (respectively with probability v an individual jumps to a new unique phenotype). Similarly an individual inherits its parent's strategy with probability $1 - u$ or adopts a strategy chosen at random among $\{C, D\}$ with probability u. Cooperation is conditional on being of the same phenotype. In other words, a C-player cooperates if the opponent is of the same phenotype, and defects otherwise. On the other hand, a D-player

always defects. Therefore, the payoffs are given by the entries of the matrix (1). For one-dimensional and infinite-dimensional phenotype spaces described above, Antal et al. (2009c) derived conditions for C to be more abundant than D under weak selection, i.e. conditions for the average frequency of C in the stationary state to strictly exceed $1/2$. In the limit of a large population the conditions are

$$(R - P)(1 + \sqrt{3}) > T - S,$$

for a one-dimensional phenotype space, and

$$R > P$$

for an infinite-dimensional phenotype spaces. These conditions are equivalent to a benefit-to-cost ratio satisfying

$$\frac{b}{c} > 1 + \frac{2}{\sqrt{3}}$$

and

$$\frac{b}{c} > 1,$$

for one-dimensional and infinite-dimensional phenotype spaces, respectively, in the case of the additive Prisoner's Dilemma with the payoff matrix (2).

However, reality lies between the two above limit cases, since a phenotype describes the similarity between individuals in several but finite characteristics (the phenotype is encoded by many genes). In this paper, we study the general case of a phenotype space of dimension $n \geq 1$. We use a perturbation method to study a mutation-selection equilibrium under weak selection. We derive a condition for C to be more abundant on average, and its large population size limit, in terms of the payoffs of the game and some identity measures. The analysis differs according to the dimension n of the phenotype space. We discuss the effect of the dimension of the phenotype space, as well as the effects of the phenotype and strategy mutation rates.

The remainder of this paper is organized as follows. In Section 2, the additive Prisoner's Dilemma in a phenotype space of any finite dimension $n \geq 1$ is presented. A condition for selection to favor cooperation in the stationary state is derived in Section 3 and a first-order approximation with respect to the intensity of selection is given in Section 4. This approximation is expressed in terms of identity measures under neutrality in Section 5. The effects of the phenotype and strategy mutation rates in the cases of $n = 2$ and $n \geq 3$ are studied in Sections 6 and 7, respectively. In Section 8, the general form of the Prisoner's Dilemma is considered. Finally, the best scenario for the evolution of cooperation stemming from the results is discussed and interpreted in Section 9.

2. Model

Consider a population consisting of N haploid individuals numbered by the integers $1, \ldots, N$. Individual k exhibits a n-dimensional phenotype represented by $\mathbf{x}(k) = (x_1(k), \ldots, x_n(k)) \in \mathbb{Z}^n$, where the ith component $x_i(k)$ is an integer for $i = 1, \ldots, n$, for $k = 1, \ldots, N$. In pairwise interactions in the context of the Prisoner's Dilemma, individual k adopts strategy $S(k) \in \{C, D\}$, where C and D refer to cooperation and defection, respectively, for $k = 1, \ldots, N$.

The system evolves according to a Wright–Fisher process. There are discrete, non-overlapping generations. Each individual of each generation is produced independently of all others by a parent chosen among the individuals of the previous generation with a probability proportional to the fitness of that parent, which is a function of the payoff that he receives (see below). An offspring inherits the strategy of its parent with probability $1 - u$ or adopts a

strategy chosen at random among the two available strategies with probability u. Note that the model with a probability u_1 of adopting the other strategy is equivalent to $u = 2u_1$. Moreover, if the parent is individual k, then the offspring inherits the phenotype $\mathbf{x}(k)$ with probability $1 - v$, adopts the phenotype $\mathbf{x}(k) + \mathbf{e}_i$ with probability $\frac{v}{2n}$, or adopts the phenotype $\mathbf{x}(k) - \mathbf{e}_i$ with probability $\frac{v}{2n}$, for $i = 1, \ldots, n$. Here, $\mathbf{e}_i \in \mathbb{Z}^n$ is a n-dimensional unit vector with the ith component equal to 1 and all other components equal to 0.

Note that a *phenotype mutation*, which occurs with probability v, corresponds to an increase or a decrease by 1 in one of the n components of the phenotype. On the other hand, a *strategy mutation*, which occurs with probability u, is parent-independent in the sense that the outcome does not depend on the strategy of the parent. Moreover, all mutation events are assumed to be independent.

Each individual engages in pairwise interactions with all other individuals of the population in the same generation and accumulates a total payoff. The result of an interaction between two individuals of the same phenotype is characterized by the 2×2 *payoff matrix* given by (2). The result of an interaction between two individuals of different phenotypes is a payoff 0 to each player. This means that cooperators play a conditional strategy: they cooperate with all the individuals who have the same phenotype, and they defect with the others. Defectors always defect. The game is assumed to be symmetric, which means that the benefit and cost payoffs are the same for every player.

The *total payoff* of a player I is given by the sum of all the payoffs that he receives, represented by a_I. The *fertility* of I is then assumed to be in the form

$$f = 1 + \delta \times a_I, \tag{3}$$

where $\delta > 0$ represents an *intensity of selection*. The *neutral model* corresponds to $\delta = 0$. Note that δ is assumed to be sufficiently small so that all fertility values are positive.

For $\mathbf{x} \in \mathbb{Z}^n$, let $n_\mathbf{x}$ denote the number of players of phenotype $\mathbf{x}$, and $m_\mathbf{x}$ the total number of cooperators of phenotype $\mathbf{x}$, respectively. Then the state of the whole population is given by the vector $\mathbf{s} = (\mathbf{n}, \mathbf{m})$, where $\mathbf{n}$ and $\mathbf{m}$ are two vectors defined by

$$\mathbf{n} = (n_\mathbf{x} : \mathbf{x} \in \mathbb{Z}^n)$$

and

$$\mathbf{m} = (m_\mathbf{x} : \mathbf{x} \in \mathbb{Z}^n).$$

Since self interaction is excluded, the total payoff of a cooperator of phenotype $\mathbf{x}$ is given by

$$a_{C,\mathbf{x}} = b(m_\mathbf{x} - 1) - c(n_\mathbf{x} - 1). \tag{4}$$

Similarly, the total payoff of a defector of phenotype $\mathbf{x}$ is

$$a_{D,\mathbf{x}} = bm_\mathbf{x}. \tag{5}$$

Note that $N = \sum_{\mathbf{y} \in \mathbb{Z}^n} n_\mathbf{y}$. The corresponding fertilities are

$$f_{C,\mathbf{x}} = 1 + \delta a_{C,\mathbf{x}} \tag{6}$$

and

$$f_{D,\mathbf{x}} = 1 + \delta a_{D,\mathbf{x}}, \tag{7}$$

respectively.

3. Condition for selection to favor cooperation

We say that *selection favors cooperation* if the expected frequency of cooperators in the stationary state strictly exceeds $1/2$ (Antal et al., 2009c). If this is ascertained at least for an intensity of selection that is small enough, then we say that *weak selection favors cooperation*.

Let $X(\mathbf{s})$ denote the frequency of cooperators in the population in state $\mathbf{s}$. The frequency of cooperators changes over one

generation by a quantity represented by $\Delta X(\mathbf{s})$. The expected value of this change can be decomposed into two terms. A first term accounts for the *change due to selection* in the absence of strategy mutation, which occurs in an expected proportion $1 - u$ of the population. A second term describes the *change due to strategy mutation* (in which case selection has no effect), which occurs in the complementary expected proportion u of the population. More precisely, we have

$$\mathbb{E}\Big[\Delta X(\mathbf{s})\Big] = (1 - u)\mathbb{E}\Big[\Delta X_{\mathrm{sel}}(\mathbf{s})\Big] + u\mathbb{E}\Big[\Delta X_{\mathrm{mut}}(\mathbf{s})\Big], \qquad (8)$$

where $\mathbf{s}$ represents the current population state. Note that Eq. (8) holds only under the assumption that strategy mutation, when it occurs, does not depend on the parental type (for more details see Allen and Tarnita (2014)). Moreover, the mutant strategy is chosen at random among the two strategies (cooperation and defection), the expected frequency of cooperators is $1/2$ after mutation, compared to $X(\mathbf{s})$ before selection and mutation. Therefore, we have

$$\mathbb{E}\Big[\Delta X_{\mathrm{mut}}(\mathbf{s})\Big] = \frac{1}{2} - X(\mathbf{s}).$$

This leads to

$$\mathbb{E}\Big[\Delta X(\mathbf{s})\Big] = (1 - u)\mathbb{E}\Big[\Delta X_{\mathrm{sel}}(\mathbf{s})\Big] + u\Big(\frac{1}{2} - X(\mathbf{s})\Big). \qquad (9)$$

In the stationary state (for the existence of the stationary state see Appendix A), the frequency of cooperators in the population, denoted by X, keeps a constant expected value. Then the expected change in the frequency of cooperators vanishes, that is

$$\mathbb{E}[\Delta X] = \mathbb{E}\Big[\mathbb{E}[\Delta X(\mathbf{s})]\Big] = 0.$$

Taking expectation on both sides of Eq. (9) yields, after rearranging terms,

$$\mathbb{E}[X] = \frac{1}{2} + \frac{1 - u}{u}\mathbb{E}[\Delta X_{\mathrm{sel}}], \qquad (10)$$

where

$$\mathbb{E}[\Delta X_{\mathrm{sel}}] = \mathbb{E}\Big[\mathbb{E}[\Delta X_{\mathrm{sel}}(\mathbf{s})]\Big].$$

We conclude that $\mathbb{E}[X] > 1/2$, which means that cooperation is favored by selection, if the expected value of the change in the frequency of cooperators due to selection only (in the absence of strategy mutation) is positive in the stationary state, that is

$$\mathbb{E}[\Delta X_{\mathrm{sel}}] > 0. \qquad (11)$$

If this inequality is ascertained at least for $\delta > 0$ small enough, then we say that cooperation is favored by weak selection.

4. Effect of selection on expected change in cooperator frequency

Given a population state $\mathbf{s} = (\mathbf{n}, \mathbf{m})$, the expected change in the frequency of cooperators due to selection before strategy mutation in offspring is given by the expression

$$\mathbb{E}\Big[\Delta X_{\mathrm{sel}}(\mathbf{s})\Big] = \frac{1}{N}\Big(\sum_{\mathbf{x} \in \mathbb{Z}^n} m_{\mathbf{x}}\omega_{C,\mathbf{x}} - m_{\mathbf{x}}\Big). \qquad (12)$$

Here, $\omega_{C,\mathbf{x}}$ is the fitness of a cooperator of phenotype $\mathbf{x}$, namely the expected number of offspring of a cooperator whose phenotype is $\mathbf{x}$, for $\mathbf{x} \in \mathbb{Z}^n$. Using the fertilities defined in Eqs. (6) and (7), we have

$$\omega_{C,\mathbf{x}} = \frac{Nf_{C,\mathbf{x}}}{\sum_{\mathbf{y} \in \mathbb{Z}^n}\Big(m_{\mathbf{y}}f_{C,\mathbf{y}} + (n_{\mathbf{y}} - m_{\mathbf{y}})f_{D,\mathbf{y}}\Big)}. \qquad (13)$$

As a matter of fact, every individual in the current generation is chosen to be the parent of an offspring in the next generation with probability given by its fertility relative to the total fertility. This is repeated independently N times. Note that the total fertility is given by

$$\sum_{\mathbf{y} \in \mathbb{Z}^n}\Big(m_{\mathbf{y}}f_{C,\mathbf{y}} + (n_{\mathbf{y}} - m_{\mathbf{y}})f_{D,\mathbf{y}}\Big)$$

$$= N + \delta(b - c)\sum_{\mathbf{y} \in \mathbb{Z}^n} m_{\mathbf{y}}(n_{\mathbf{y}} - 1). \qquad (14)$$

A first-order approximation with respect to the intensity of selection δ yields the following expression for the expected number of offspring of a cooperator whose phenotype is $\mathbf{x}$:

$$\omega_{C,\mathbf{x}} = 1 + \delta\Big[b(m_{\mathbf{x}} - 1) - c(n_{\mathbf{x}} - 1) - \frac{b - c}{N}\sum_{\mathbf{y} \in \mathbb{Z}^n} m_{\mathbf{y}}(n_{\mathbf{y}} - 1)\Big]$$

$$+ o(\delta). \qquad (15)$$

Therefore, Eq. (12) becomes

$$\mathbb{E}\Big[\Delta X_{\mathrm{sel}}(\mathbf{s})\Big] = \frac{\delta}{N}\Big[b\sum_{\mathbf{x} \in \mathbb{Z}^n} m_{\mathbf{x}}(m_{\mathbf{x}} - 1) - c\sum_{\mathbf{x} \in \mathbb{Z}^n} m_{\mathbf{x}}(n_{\mathbf{x}} - 1)$$

$$- \frac{b - c}{N}\sum_{\mathbf{x}, \mathbf{y} \in \mathbb{Z}^n} m_{\mathbf{x}}m_{\mathbf{y}}(n_{\mathbf{y}} - 1)\Big] + o(\delta). \qquad (16)$$

Taking expectation on both sides of the above equation gives a first-order approximation with respect to δ for the expected change in frequency of cooperators under weak selection given by

$$\mathbb{E}\Big[\Delta X_{\mathrm{sel}}\Big] = \frac{\delta}{N}\Big[b\sum_{\mathbf{x} \in \mathbb{Z}^n}\mathbb{E}_0\Big(m_{\mathbf{x}}(m_{\mathbf{x}} - 1)\Big) - c\sum_{\mathbf{x} \in \mathbb{Z}^n}\mathbb{E}_0\Big(m_{\mathbf{x}}(n_{\mathbf{x}} - 1)\Big)$$

$$- \frac{b - c}{N}\sum_{\mathbf{x}, \mathbf{y} \in \mathbb{Z}^n}\mathbb{E}_0\Big(m_{\mathbf{x}}m_{\mathbf{y}}(n_{\mathbf{y}} - 1)\Big)\Big] + o(\delta). \qquad (17)$$

Here, E_0 denotes expectation in the stationary state under neutrality ($\delta = 0$).

5. Condition for weak selection to favor cooperation in terms of identity measures

For an event A, let us introduce the indicator variable

$$\mathbb{1}_A = \begin{cases} 1 & \text{if the event } A \text{ is true,} \\ 0 & \text{if the event } A \text{ is false.} \end{cases}$$

In a population with individuals exhibiting phenotype $\mathbf{x}(k)$ and playing strategy $S(k)$, for $k = 1, \ldots, N$, the number of individuals of phenotype $\mathbf{x}$, given by $n_{\mathbf{x}}$, and the number of cooperators of phenotype $\mathbf{x}$, given by $m_{\mathbf{x}}$, can be expressed as

$$n_{\mathbf{x}} = \sum_{k=1}^{N} \mathbb{1}_{\{\mathbf{x}(k)=\mathbf{x}\}}$$

and

$$m_{\mathbf{x}} = \sum_{k=1}^{N} \mathbb{1}_{\{\mathbf{x}(k)=\mathbf{x}\}}\mathbb{1}_{\{S(k)=C\}}.$$

Moreover, we have:

$$\sum_{\mathbf{x} \in \mathbb{Z}^n} m_{\mathbf{x}} = \sum_{\mathbf{x} \in \mathbb{Z}^n}\sum_{k=1}^{N} \mathbb{1}_{\{\mathbf{x}(k)=\mathbf{x}\}}\mathbb{1}_{\{S(k)=C\}} = \sum_{k=1}^{N} \mathbb{1}_{\{S(k)=C\}},$$

$$\sum_{\mathbf{x} \in \mathbb{Z}^n} m_{\mathbf{x}}^2 = \sum_{\mathbf{x} \in \mathbb{Z}^n}\sum_{k,j=1}^{N} \mathbb{1}_{\{\mathbf{x}(k)=\mathbf{x}(j)=\mathbf{x}\}}\mathbb{1}_{\{S(k)=S(j)=C\}}$$

$$= \sum_{k,j=1}^{N} \mathbb{1}_{\{\mathbf{x}(k)=\mathbf{x}(j)\}} \mathbb{1}_{\{S(k)=S(j)=C\}},$$

$$\sum_{\mathbf{x},\mathbf{y}\in\mathbb{Z}^n} m_\mathbf{x} m_\mathbf{y} = \sum_{\mathbf{x},\mathbf{y}\in\mathbb{Z}^n} \sum_{k,j=1}^{N} \mathbb{1}_{\{\mathbf{x}(k)=\mathbf{x}\}} \mathbb{1}_{\{\mathbf{x}(j)=\mathbf{y}\}} \mathbb{1}_{\{S(k)=S(j)=C\}}$$

$$= \sum_{k,j=1}^{N} \mathbb{1}_{\{S(k)=S(j)=C\}},$$

$$\sum_{\mathbf{x}\in\mathbb{Z}^n} m_\mathbf{x} n_\mathbf{x} = \sum_{\mathbf{x}\in\mathbb{Z}^n} \sum_{k,j=1}^{N} \mathbb{1}_{\{\mathbf{x}(k)=\mathbf{x}(j)=\mathbf{x}\}} \mathbb{1}_{\{S(k)=C\}}$$

$$= \sum_{k,j=1}^{N} \mathbb{1}_{\{\mathbf{x}(k)=\mathbf{x}(j)\}} \mathbb{1}_{\{S(k)=C\}},$$

$$\sum_{\mathbf{x},\mathbf{y}\in\mathbb{Z}^n} m_\mathbf{x} m_\mathbf{y} n_\mathbf{y} = \sum_{\mathbf{x},\mathbf{y}\in\mathbb{Z}^n} \sum_{k,j,l=1}^{N} \mathbb{1}_{\{\mathbf{x}(k)=\mathbf{x}\}} \mathbb{1}_{\{S(k)=S(j)=C\}} \mathbb{1}_{\{\mathbf{x}(j)=\mathbf{x}(l)=\mathbf{y}\}}.$$

Using the fact that the two strategies C and D are interchangeable in the neutral model ($\delta = 0$), we have the following equalities:

$$\mathbb{E}_0[\mathbb{1}_{\{S(k)=C\}}] = \frac{1}{2}\mathbb{E}_0[\mathbb{1}_{\{S(k)=C\}} + \mathbb{1}_{\{S(k)=D\}}] = 1/2,$$

$$\mathbb{E}_0[\mathbb{1}_{\{S(k)=S(j)=C\}}] = \frac{1}{2}\mathbb{E}_0[\mathbb{1}_{\{S(k)=S(j)\}}] = y_n/2,$$

$$\mathbb{E}_0[\mathbb{1}_{\{\mathbf{x}(k)=\mathbf{x}(j)\}}] = z_n,$$

$$\mathbb{E}_0[\mathbb{1}_{\{\mathbf{x}(k)=\mathbf{x}(j)\}} \mathbb{1}_{\{S(k)=S(j)=C\}}] = \frac{1}{2}\mathbb{E}_0[\mathbb{1}_{\{\mathbf{x}(k)=\mathbf{x}(j)\}} \mathbb{1}_{\{S(k)=S(j)\}}] = g_n/2,$$

$$\mathbb{E}_0[\mathbb{1}_{\{\mathbf{x}(k)=\mathbf{x}(j)\}} \mathbb{1}_{\{S(j)=S(l)=C\}}] = \frac{1}{2}\mathbb{E}_0[\mathbb{1}_{\{\mathbf{x}(k)=\mathbf{x}(j)\}} \mathbb{1}_{\{S(j)=S(l)\}}] = h_n/2.$$

Here, the integers k, j and l designate three distinct individuals chosen at random in the population in the stationary state, while y_n, z_n, g_n and h_n are identity measures defined as follows:

$y_n = \mathbb{P}_0[k \text{ and } j \text{ have the same strategy}],$
$z_n = \mathbb{P}_0[k \text{ and } j \text{ have the same phenotype}],$
$g_n = \mathbb{P}_0[k \text{ and } j \text{ have the same strategy and the same phenotype}],$
$h_n = \mathbb{P}_0[j \text{ and } l \text{ have the same strategy while } k \text{ and } j$
    have the same phenotype].

The notation $\mathbb{P}_0$ is used for probability under neutrality. In terms of these identity measures, we have:

$$\mathbb{E}_0\left[\sum_{\mathbf{x}\in\mathbb{Z}^n} m_\mathbf{x}\right] = N/2,$$

$$\mathbb{E}_0\left[\sum_{\mathbf{x}\in\mathbb{Z}^n} m_\mathbf{x}^2\right] = \frac{N}{2} + \frac{N(N-1)}{2}g_n,$$

$$\mathbb{E}_0\left[\sum_{\mathbf{x},\mathbf{y}\in\mathbb{Z}^n} m_\mathbf{x} m_\mathbf{y}\right] = \frac{N}{2} + \frac{N(N-1)}{2}y_n,$$

$$\mathbb{E}_0\left[\sum_{\mathbf{x}\in\mathbb{Z}^n} m_\mathbf{x} n_\mathbf{x}\right] = \frac{N}{2} + \frac{N(N-1)}{2}z_n,$$

$$\mathbb{E}_0\left[\sum_{\mathbf{x},\mathbf{y}\in\mathbb{Z}^n} m_\mathbf{x} m_\mathbf{y} n_\mathbf{y}\right] = \frac{N}{2} + \frac{N(N-1)}{2}(y_n + z_n + g_n)$$
$$+ \frac{N(N-1)(N-2)}{2}h_n.$$

Hence, following (11) and (17), a condition for weak selection to favor cooperation is

$$\Big((N-2)(g_n-h_n) + g_n - z_n\Big)b$$

$$- \Big((N-2)(z_n-h_n) + z_n - g_n\Big)c > 0. \tag{18}$$

This condition is equivalent to

$$\frac{b}{c} > \beta_n, \tag{19}$$

where the threshold benefit-to-cost ratio β_n is a function of the identity measures z_n, g_n and h_n, besides the population size N, given by

$$\beta_n = \frac{(N-2)(z_n-h_n) + z_n - g_n}{(N-2)(g_n-h_n) + g_n - z_n}. \tag{20}$$

This expression is valid for any population size $N \geq 3$.

Remark 5.1. In the case of a population size $N = 2$, condition (18) for weak selection to favor cooperation never holds with the payoff matrix (2) for the additive Prisoner's Dilemma, since the payoff b that a defector receives against a cooperator is always greater than the payoff $-c$ that a cooperator receives against a defector.

We consider the limiting case of a large population size and low mutation rates so that the population-scaled strategy mutation rate $\mu = Nu$ and the population-scaled phenotype mutation rate $\nu = N\nu$ remain constant as $N \to \infty$. In this limiting case, the threshold ratio (20) becomes

$$\beta_n = \frac{z_n - h_n}{g_n - h_n}. \tag{21}$$

Now, we use the expressions (see Appendix B)

$$z_n = \frac{n}{2\nu} G_n\left(\frac{1}{2\nu}\right), \tag{22a}$$

$$g_n = \frac{n}{4\nu}\left\{G_n\left(\frac{1}{2\nu}\right) + G_n\left(\frac{2\mu+1}{2\nu}\right)\right\}, \tag{22b}$$

$$h_n = \frac{n}{8\nu}\left\{\frac{3+2\mu}{1+\mu}G_n\left(\frac{1}{2\nu}\right) + G_n\left(\frac{1+2\mu}{2\nu}\right)\right.$$
$$\left. - \frac{\mu(3+2\mu)}{(1+\mu)(1+2\mu)}G_n\left(\frac{3+2\mu}{2\nu}\right)\right\}. \tag{22c}$$

These expressions are given in terms of G_n, the Laplace transform of the Modified Bessel function of power n. This transform is defined as

$$G_n(x) = \int_0^\infty \Big(I_0(\sigma)\Big)^n e^{-n(1+x)\sigma} d\sigma. \tag{23}$$

Here, I_0 denotes the Modified Bessel function of index 0 given by the expansion

$$I_0(x) = \sum_{l=0}^\infty \frac{1}{(l!)^2}\left(\frac{x}{2}\right)^{2l}. \tag{24}$$

By substituting the expressions (22a), (22b) and (22c) for z_n, g_n and h_n, respectively, the threshold ratio (21) takes the form

β_n

$$= \frac{(1+2\mu)^2 G_n\left(\frac{1}{2\nu}\right) + \mu(3+2\mu)G_n\left(\frac{3+2\mu}{2\nu}\right) - (1+\mu)(1+2\mu)G_n\left(\frac{1+2\mu}{2\nu}\right)}{-(1+2\mu)G_n\left(\frac{1}{2\nu}\right) + \mu(3+2\mu)G_n\left(\frac{3+2\mu}{2\nu}\right) + (1+\mu)(1+2\mu)G_n\left(\frac{1+2\mu}{2\nu}\right)}. \tag{25}$$

Note that $G_n(x)$ is a decreasing function on $(0, +\infty)$, since $e^{-n(1+x)\sigma}$ is decreasing on $(0, +\infty)$ as a function of x for every $\sigma \in (0, +\infty)$. Therefore, the difference between the numerator and the denominator in (25) is given by

$$2(1+2\mu)(1+\mu)\left(G_n\left(\frac{1}{2\nu}\right) - G_n\left(\frac{1+2\mu}{2\nu}\right)\right) > 0.$$

This means that the threshold ratio β_n strictly exceeds 1, for any population-scaled strategy mutation rate $\mu > 0$ and any population-scaled phenotype mutation rate $\nu > 0$ in the limit of a large population size ($N \to \infty$).

In the remainder of the paper, we are interested in the best scenario for the evolution of cooperation. More precisely, we look for the values of μ and ν that minimize the threshold ratio β_n.

The case of a one-dimensional phenotype space ($n = 1$) is studied in Antal et al. (2009c). It is shown that the best scenario for the evolution of cooperation under the additive Prisoner's Dilemma stems from a high population-scaled phenotype mutation rate ($\nu \to \infty$) and a low population-scaled strategy mutation rate ($\mu \to 0$) with a threshold ratio $\beta_1 = 1 + \frac{2}{\sqrt{3}}$.

For a phenotype space of dimension $n \geq 2$ studied here, the analysis is different from the case $n = 1$ and differs according to two cases: the case where $G_n(x)$ has an infinite right-hand limit at 0, which holds for a phenotype space of dimension $n = 2$, and the case where $G_n(x)$ has a finite right-hand limit at 0, which holds for a phenotype space of dimension $n \geq 3$.

6. Bidimensional phenotype space ($n = 2$)

In this section, we study the best scenario for the evolution of cooperation in the case of a phenotype space of dimension $n = 2$. First note that the Modified Bessel function of index 0 given by (24) satisfies

$$\left(I_0(x)\right)^2 = \sum_{l=0}^{\infty} \sum_{l'=0}^{l} \frac{1}{(l'!)^2} \cdot \frac{1}{((l-l')!)^2} \left(\frac{x}{2}\right)^{2l}$$
$$= \sum_{l=0}^{\infty} \frac{\binom{2l}{l}}{(l!)^2} \left(\frac{x}{2}\right)^{2l}. \tag{26}$$

This expansion and the identity

$$\int_0^{\infty} \tau^{2l} e^{-a\tau} d\tau = \frac{(2l)!}{a^{2l+1}}$$

lead to

$$G_2(x) = \int_0^{\infty} \left(I_0(\tau)\right)^2 e^{-2(1+x)\tau} d\tau$$
$$= \sum_{l=0}^{\infty} \frac{\binom{2l}{l}}{2^{2l}(l!)^2} \int_0^{\infty} \tau^{2l} e^{-2(1+x)\tau} d\tau$$
$$= \frac{1}{2(1+x)} \sum_{l=0}^{\infty} \binom{2l}{l}\binom{2l}{l} \left(\frac{1}{4(1+x)}\right)^{2l}$$
$$= \frac{1}{\pi(1+x)} K\left(\frac{1}{1+x}\right). \tag{27}$$

Here, K denotes the Legendre complete elliptic integral of the first kind (Erdélyi et al., 1981) given by the series expansion

$$K(x) = \frac{\pi}{2} \sum_{l=0}^{\infty} \binom{2l}{l}\binom{2l}{l}\left(\frac{x}{4}\right)^{2l}, \tag{28}$$

for $|x| < 1$. We are interested in the threshold benefit-to-cost ratio (25) in the case where $\nu \to \infty$. We note that $K(x)$ has an infinite left-hand limit at 1, that is

$$\lim_{x \to 1^-} K(x) = +\infty,$$

so that $G_2(x)$ has an infinite right-hand limit at 0, that is

$$\lim_{x \to 0^+} G_2(x) = +\infty.$$

Actually the asymptotic behavior of $K(x)$ as $x \to 1^-$ (Erdélyi et al., 1981) is described by

$$K(x) = 4 \log\left(\frac{4}{\sqrt{1-x^2}}\right) + o(1), \tag{29}$$

where $o(1)$ is a function of x, which has the following limit

$$\lim_{x \to 1^-} o(1) = 0.$$

From Eq. (27), this leads to

$$G_2\left(\frac{a}{2\nu}\right) = \frac{2\nu}{\pi(a+2\nu)} K\left(\frac{2\nu}{a+2\nu}\right)$$
$$= \frac{4}{\pi} \log \frac{4(a+2\nu)}{\sqrt{a^2+4a\nu}} + o(1)$$
$$= \frac{4}{\pi} \log\left(\frac{\sqrt{\nu}}{\sqrt{a}}\left(1 + \frac{3a}{8\nu} + o(\nu^{-1})\right)\right) + o(1)$$
$$= \frac{2\log\nu}{\pi} + o(\log\nu), \tag{30}$$

as $\nu \to \infty$ for any $a > 0$. Here, $o(\log\nu)$ is a function of ν such that

$$\lim_{\nu \to \infty} \frac{o(\log\nu)}{\log\nu} = 0.$$

Therefore, Eq. (25) for $n = 2$ takes the form

$$\beta_2$$
$$= \frac{\left((1+2\mu)^2 + \mu(3+2\mu) - (1+\mu)(1+2\mu)\right)2\log\nu + o(\log\nu)}{\left(-(1+2\mu) + \mu(3+2\mu) + (1+\mu)(1+2\mu)\right)2\log\nu + o(\log\nu)}$$
$$= 1 + o(1), \tag{31}$$

where $o(1)$ is a non negative function of ν that tends to 0 as $\nu \to \infty$. This means that the value of the threshold benefit-to-cost ratio β_2 in the limit $\nu \to \infty$ equals 1. Therefore, in the case of the additive Prisoner's Dilemma in a 2-dimensional phenotype space, cooperation is favored by weak selection as $\nu \to \infty$ whenever the benefit b from cooperation is larger than its cost c, that is $b > c$.

Conversely, using the expansion of K given by (28), we obtain

$$K(x) = \frac{\pi}{2} + \frac{\pi x^2}{8} + o(x^2), \tag{32}$$

as $x \to 0$. Then we have

$$G_2\left(\frac{a}{2\nu}\right) = \frac{\nu}{a} - \frac{2\nu^2}{a^2} + o(\nu^2),$$

as $\nu \to 0$, for any $a > 0$. This entails that

$$\beta_2 = \frac{(1+2\mu)(3+2\mu)}{4(1+\mu)\nu} + o(1), \tag{33}$$

as $\nu \to 0$. Then the threshold benefit-to-cost ratio β_2 diverges as $\frac{(1+2\mu)(3+2\mu)}{4(1+\mu)\nu}$ for small ν. Consequently, a small scaled-population rate of phenotype mutation opposes cooperators to evolve in a two-dimensional phenotype space.

Figs. 1 and 2 illustrate the effects of the population-scaled mutation rates ν and μ for phenotype and strategy, respectively, on the threshold benefit-to-cost ratio β_2 given by (25) in the case of phenotype space of dimension $n = 2$ in the limit of a large population size. These figures show that the threshold ratio β_2 is decreasing as a function of ν and increasing as a function of μ. This means that the condition for cooperation to be favored is less stringent if ν is larger. Moreover, for intermediate values of $0 < \nu < \infty$, this condition is less stringent for smaller values of μ. Note that the threshold ratio $\beta_2 \to 1$ as $\nu \to \infty$, while $\beta_2 \to \infty$ as $\nu \to 0$.

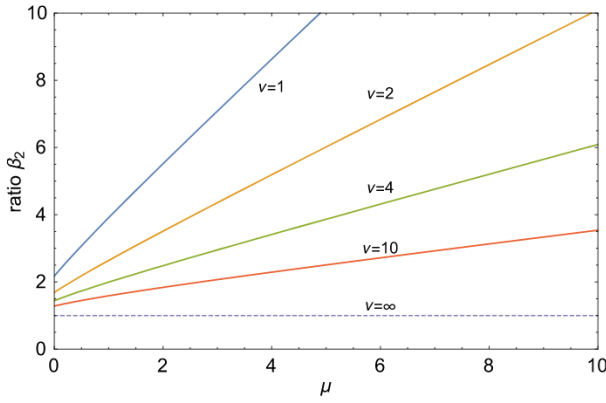**Fig. 1.** Exact threshold benefit-to-cost ratio β_2 in the $N \to \infty$ limit as a function of the population-scaled strategy mutation rate $\mu = N u$ for different values of the population-scaled phenotype mutation rate $\nu = N v$. Cooperation is most favored in the $\nu \to \infty$ limit, where $\beta_2 \to 1$.
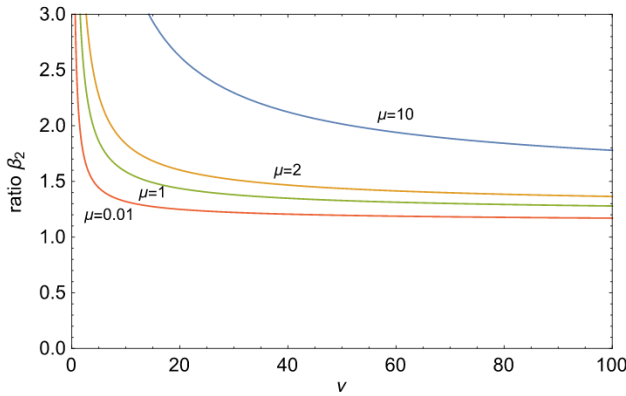

Fig. 2. Exact threshold benefit-to-cost ratio β_2 in the $N \to \infty$ limit as a function of the population-scaled phenotype mutation rate $\nu = N v$ for different values of the population-scaled strategy mutation rate $\mu = N u$. The worst scenario for the evolution of cooperation is when $\nu \to 0$, where $\beta_2 \to \infty$.

7. Phenotype space of dimension $n \geq 3$

The Modified Bessel function $I_0(\tau)$ has an asymptotic behavior as $\tau \to \infty$ (Watson, 1944) given by

$$I_0(\tau) \approx \frac{e^\tau}{\sqrt{2\pi\tau}},$$

which entails that

$$(I_0(\tau))^n e^{-n\tau} \approx \frac{1}{(\sqrt{2\pi\tau})^n}.$$

This guarantees that $\int_0^\infty (I_0(\tau))^n e^{-n\tau} d\tau$ exists for $n \geq 3$. Hence, the dominated convergence theorem ensures that

$$\lim_{x \to 0^+} G_n(x) = \int_0^\infty (I_0(\tau))^n e^{-n\tau} d\tau,$$

since

$$\lim_{x \to 0^+} (I_0(\tau))^n e^{-n\tau(1+x)} = (I_0(\tau))^n e^{-n\tau}$$

and

$$|(I_0(\tau))^n e^{-n\tau(1+x)}| \leq (I_0(\tau))^n e^{-n\tau},$$

for all $\tau \geq 0$. Then, $G_n(x)$ has a right-hand limit at 0 given by

$$G_n(0^+) = \int_0^\infty (I_0(\tau))^n e^{-n\tau} d\tau.$$

As $\nu \to \infty$, we have

$$\lim_{\nu \to \infty} G_2\left(\frac{1}{2\nu}\right) = \lim_{\nu \to \infty} G_2\left(\frac{1+2\mu}{2\nu}\right)$$

$$= \lim_{\nu \to \infty} G_2\left(\frac{3+2\mu}{2\nu}\right) = G_n(0^+), \tag{34}$$

and therefore,

$$\lim_{\nu \to \infty} \beta_n$$

$$= \frac{(1+2\mu)^2 G_n(0^+) + \mu(3+2\mu)G_n(0^+) - (1+\mu)(1+2\mu)G_n(0^+)}{-(1+2\mu)G_n(0^+) + \mu(3+2\mu)G_n(0^+) + (1+\mu)(1+2\mu)G_n(0^+)}$$

$$= 1. \tag{35}$$

Then, with the payoff matrix (2) for the additive Prisoner's Dilemma with $b > c$, the expected frequency of cooperators in the stationary state under weak selection strictly exceeds $1/2$, which means that cooperation is more abundant then defection.

Now we study the effect of a small population-scaled phenotype mutation rate on the threshold benefit-to-cost ratio β_n. First, from Eq. (24) we have the asymptotic expansion

$$I_0(t) = 1 + \frac{t^2}{4} + o(t^2), \tag{36}$$

as $t \to 0$. Then using this expansion in (23) gives the asymptotic expansion

$$G_n\left(\frac{a}{2\nu}\right) = \frac{2\nu}{2\nu + a} \int_0^\infty \left(I_0\left(\frac{2\nu\sigma}{2\nu + a}\right)\right)^n e^{-n\sigma} d\sigma$$

$$= \frac{2\nu}{2\nu + a} \int_0^\infty \left(1 + \frac{n\nu^2\sigma^2}{a^2} + o(\nu^2)\right) e^{-n\sigma} d\sigma$$

$$= \frac{2\nu}{na} - \frac{4\nu^2}{na^2} + o(\nu^2),$$

as $\nu \to 0$, for any $a > 0$. This yields the asymptotic expression

$$\beta_n = \frac{(1+2\mu)(3+2\mu)}{4(1+\mu)\nu} + o(1), \tag{37}$$

as $\nu \to 0$. Then the ratio β_n diverges as $\frac{(1+2\mu)(3+2\mu)}{4(1+\mu)\nu}$ as $\nu \to 0$, which means that a scaled-population phenotype mutation rate that is small enough opposes evolution of cooperation. To see the effect of the scaled-population strategy mutation rate on the ratio β_n, note that $\frac{(1+2\mu)(3+2\mu)}{4(1+\mu)\nu}$ is an increasing function of μ. Therefore, a smaller scaled-population strategy mutation rate is more favorable for cooperation to evolve. Note that the dimension of the phenotype space n has no effect on the first term of (37), but it has an effect on the second term which is of order $o(1)$.

The same qualitative conclusions hold for a phenotype space of dimension $n \geq 3$ as for the case $n = 2$. As a function of the population-scaled phenotype mutation rate ν, the threshold benefit-to-cost ratio β_n is decreasing. However, the threshold ratio β_n is increasing with respect to the population-scaled strategy mutation rate μ.

8. General case

In this section, we study the case of the general Prisoner's Dilemma. More precisely, an interaction between two individuals of the same phenotype is characterized by the 2×2 *payoff matrix* given by (1). The result of an interaction between two individuals of different phenotypes is a payoff P to each player. A similar reasoning to the one given in Sections 4 and 5 yields as condition for weak selection to favor cooperation

$$M_1 R + M_2 S + M_3 P + M_4 T > 0, \tag{38}$$

where

$$M_1 = \left(1 - \frac{2}{N}\right)(g_n - \eta_n),$$

$$M_2 = \left(1 - \frac{1}{N}\right)(z_n - g_n) - \left(1 - \frac{2}{N}\right)(h_n - \eta_n),$$

$$M_3 = \left(1 - \frac{2}{N}\right)\left(2h_n - \eta_n - z_n\right),$$

$$M_4 = \left(1 - \frac{2}{N}\right)\left(\eta_n - h_n\right) - \frac{1}{N}\left(z_n - g_n\right).$$

Here, η_n is the identity measure defined by

$$\eta_n = \mathbb{P}_0\Big[k, j \text{ and } l \text{ have the same strategy while } k \text{ and } j$$

$$\text{have the same phenotype}\Big],$$

where k, j and l are three individuals chosen at random without replacement in the stationary state under neutrality. Condition (38) is valid for any population size $N \geq 2$ and any dimension $n \geq 1$ for the phenotype space. In the limit of a large population, this condition becomes

$$(R - S)g_n + (S - P)z_n > (R - S - T + P)\eta_n$$
$$+ (S + T - 2P)h_n. \qquad (39)$$

Now, by using the expression (see Appendix B)

$$\eta_n = \frac{n}{8\nu}\left\{\frac{2+\mu}{1+\mu}G_n\left(\frac{1}{2\nu}\right) + 2G_n\left(\frac{1+2\mu}{2\nu}\right)\right.$$

$$\left. - \frac{\mu(3+2\mu)}{(1+\mu)(1+2\mu)}G_n\left(\frac{3+2\mu}{2\nu}\right)\right\}, \qquad (40)$$

and the expressions (22a), (22b), (22c) for z_n, g_n and h_n, condition (39) can be written in the form

$$\sigma_n R + S > T + \sigma_n P, \qquad (41)$$

where

$$\sigma_n = \frac{\mu\left((1+2\mu)G_n(\frac{1}{2\nu}) + (3+2\mu)G_n(\frac{3+2\mu}{2\nu})\right)}{(1+\mu)(1+2\mu)\left(G_n(\frac{1}{2\nu}) - G_n(\frac{1+2\mu}{2\nu})\right)}. \qquad (42)$$

Here, σ_n is a *structure coefficient* (Tarnita et al., 2009), which does not depend on the entries of the payoff matrix. Alternatively, σ_n can be expressed as

$$\sigma_n = \frac{\beta_n + 1}{\beta_n - 1}. \qquad (43)$$

Thus, if the critical benefit-to-cost ratio β_n is known, we can immediately obtain σ_n and vice versa.

Now, we are interested in the condition to favor cooperation in the $\nu \to \infty$ limit in the general case. The fact that $\lim_{\nu\to\infty} \beta_n = 1$ and relation (43) guaranty that $\lim_{\nu\to\infty} \sigma_n = \infty$. Then, the condition for weak selection to favor cooperation takes the simple form

$$R > P, \qquad (44)$$

as $\nu \to \infty$, for any population-scaled mutation rate $\mu > 0$. This condition is valid for a phenotype space of any dimension $n \geq 2$. The condition means that weak selection favors the strategy with the higher payoff against itself. This condition is the well-known condition for *Pareto dominance* to prevail over risk dominance in coordination games (Harsanyi and Selten, 1988). In this case, the diagonal entries of the payoff matrix are more important than the off-diagonal entries for determining the best strategy.

As the population-scaled phenotype mutation rate tends to 0, the structure coefficient tends to 1 that is $\lim_{\nu\to0} \sigma_n = 1$, owing

to relation (43) and the fact that $\lim_{\nu\to0} \beta_n = \infty$. Then, condition (41) for weak selection to favor cooperation becomes

$$R + S > T + P,$$

as $\nu \to 0$. This condition is valid for any population-scaled mutation rate $\mu > 0$ and for any phenotype space dimension $n \geq 2$. This is the well-known condition for risk dominance in a coordination game (Harsanyi and Selten, 1988). Here, the situation is equivalent to a well-mixed population and then the structure of the phenotype space has no effect on the favored strategy.

9. Discussion

We have derived conditions that favor the evolution of cooperation in a phenotype space of any finite dimension $n \geq 2$. Consider a population of N individuals labeled by the integers $1, \ldots, N$. Each individual has a phenotype represented by a n-dimensional vector with integer components. Moreover, each individual adopts one of two strategies, cooperation and defection. Generations are discrete and non overlapping. The phenotype mutation rate is v. If the phenotype of the parent k is $\mathbf{x}(k)$, then the phenotype of an offspring of k is $\mathbf{x}(k) - \mathbf{e}_i$, $\mathbf{x}(k)$ or $\mathbf{x}(k) + \mathbf{e}_i$ with probability $\frac{v}{2n}$, $1 - v$ or $\frac{v}{2n}$, respectively, for $i = 1, \ldots, n$. Here, $\mathbf{e}_i$ denotes the n-dimensional vector with 1 in the ith component and 0 elsewhere. We assume also that an offspring inherits the strategy of its parent with probability $1 - u$ and chooses a strategy at random among cooperation and defection with probability u. Every individual interacts with all the other individuals in the same generation to accumulate a total payoff, which affects its contribution to the next generation by a small additive amount proportional to some intensity of selection, called its fertility. A cooperator receives a payoff R or S against a cooperator or a defector, respectively, while a defector receives a payoff T or P, respectively, against the corresponding players. It is assumed that $T > R > P > S$, which corresponds to the Prisoner's Dilemma. Moreover, cooperation is played only against an individual of the same phenotype.

We have shown that weak selection favors cooperation in the sense that it is more abundant on average in the stationary state, if a relation in the form

$$M_1 R + M_2 S + M_3 P + M_4 T > 0 \qquad (45)$$

holds. This condition is given in terms of the payoffs R, S, T, P weighted by some coefficients M_i for $i = 1, 2, 3, 4$. These depend only on identity measures under neutrality besides the population size $N \geq 2$.

In the limit of a large population, the condition for cooperation to be more abundant on average in the stationary state under weak selection becomes

$$(R - S)g_n + (S - P)z_n > (R - S - T + P)\eta_n$$
$$+ (S + T - 2P)h_n, \qquad (46)$$

where z_n, g_n, h_n and η_n are identity measures under neutrality derived in Appendix B. These identity measures are similar to the ones that arise in studies of social behavior (Hamilton, 1964a,b). The first three correspond to the traditional genetic measures F, ϕ and γ, respectively, used in Rousset and Roze (2007) and Lehmann et al. (2009). The above condition can be written in the form

$$\sigma_n R + S > \sigma_n P + T, \qquad (47)$$

where σ_n, called a structure coefficient (Tarnita et al., 2009), depends on the population-scaled phenotype mutation rate $\nu = N v$ and the population-scaled strategy mutation rate $\mu = Nu$, but does not depend on the payoffs. This parameter σ_n quantifies the degree to which individuals using the same strategy are more or less likely to interact than individuals using different strategies.

In the limit of a low population-scaled phenotype mutation rate ($\nu \to 0$), we have shown that the structure coefficient σ_n tends to 1 for $n \geq 2$. Then the condition that favors the evolution of cooperation becomes

$$R + S > T + P.$$

This is the well-known condition for risk dominance in a coordination game (Harsanyi and Selten, 1988), which is a typical condition for two player games in non-structured populations.

However, in the limit of a large population-scaled phenotype mutation rate ($\nu \to \infty$), we have shown that the structure coefficient σ_n tends to ∞ for $n \geq 2$. In this case, the condition for weak selection to favor the evolution of cooperation takes the form

$$R > P.$$

This means that weak selection favors the strategy with the higher payoff against itself. The intuitive reason is that in the limit $\nu \to \infty$ phenotypic identity entails strategic identity, which means that individuals with the same phenotype use the same strategy. For $n = 2$, the expression (30) for the Laplace transform of the Modified Bessel function of power 2 in the identity measures (22a) and (22b) leads to

$$z_2 = \frac{2 \log \nu}{\pi \nu} + o\left(\frac{\log \nu}{\nu}\right),$$

$$g_2 = \frac{2 \log \nu}{\pi \nu} + o\left(\frac{\log \nu}{\nu}\right),$$

while the expression (34) in the identity measures (22a) and (22b) leads to

$$z_n = \frac{n}{2\nu} G_n(0^+) + o\left(\frac{1}{\nu}\right),$$

$$g_n = \frac{n}{2\nu} G_n(0^+) + o\left(\frac{1}{\nu}\right),$$

for $n \geq 3$. These expressions imply that $\lim_{\nu \to \infty} z_n / g_n = 1$, which conveys the idea that *phenotypic identity entails strategic identity*. In this case, the population is subdivided into homogeneous groups, that is, groups of cooperators and groups of defectors. Then the strategy with the higher payoff against itself is favored.

In the case of the additive Prisoner's Dilemma with a phenotype space of any finite dimension, condition (47) is equivalent to a benefit-to-cost ratio b/c strictly exceeding some threshold value β_n given by

$$\frac{b}{c} > \beta_n = \frac{z_n - h_n}{g_n - h_n}. \tag{48}$$

There is a relation between the structure coefficient and the threshold benefit-to-cost ratio given by

$$\beta_n = \frac{\sigma_n + 1}{\sigma_n - 1}.$$

We have derived in Sections 6 and 7 the best scenario in favor of the evolution of cooperation. This scenario is determined by the values of the population-scaled strategy mutation rate μ and phenotype mutation rate ν which minimize β_n, for $n \geq 2$. For a one-dimensional phenotype space ($n = 1$), Antal et al. (2009c) showed that the best scenario was given by $\nu = N\upsilon \gg 1$ AND $\mu = Nu \ll 1$. In this case, the threshold value for the benefit-to-cost ratio is

$$\beta_1 = 1 + \frac{2}{\sqrt{3}}.$$

In this paper, we have shown that, for a phenotype space of dimension $n \geq 2$, the best scenario is given by $\nu = N\upsilon \gg 1$. In this case, the threshold value is

$$\beta_n = 1.$$

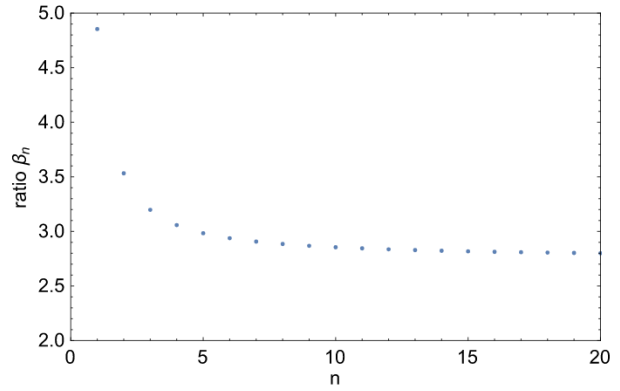**Fig. 3.** Exact threshold benefit-to-cost ratio β_n in the $N \to \infty$ limit with $\nu = 1$ and $\mu = 1$ as a function of the dimension n of the phenotype space. The ratio β_n is a decreasing function in n. Cooperation is most favored in the $n \to \infty$ limit, where $\beta_\infty = 2.75$.
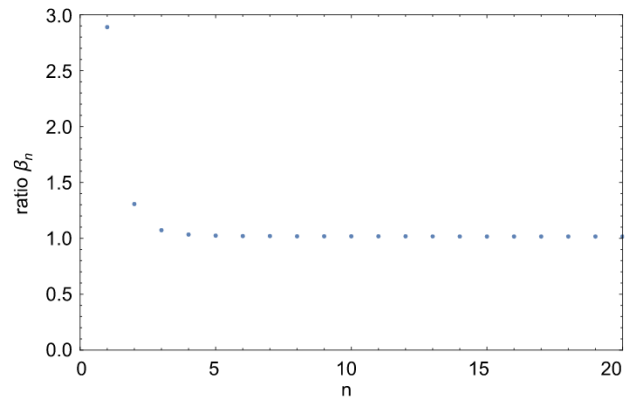

Fig. 4. Exact threshold benefit-to-cost ratio β_n in the $N \to \infty$ limit with $\nu = 100$ and $\mu = 1$ as a function of the dimension n of the phenotype space. The ratio β_n is a decreasing function in n. Cooperation is most favored in the $n \to \infty$ limit, where $\beta_\infty \approx 1.015$.

This condition corresponds to the best scenario in Antal et al. (2009c) for $n = \infty$. In particular, this condition implies that weak selection favors cooperation whenever the benefit b from cooperation is larger than the cost c.

In general, the threshold value β_n that the benefit-to-cost ratio must exceed for weak selection to favor cooperation is a decreasing function with respect to the dimension n of the phenotype space for any population-scaled phenotype mutation rate ν and any population-scaled strategy mutation rate μ. This is illustrated in Figs. 3 and 4. This suggests that a higher dimension of the phenotype space is more favorable to the evolution of cooperation. Fig. 3 shows the threshold ratio β_n as a function of the phenotype space dimension for $\mu = 1$ and $\nu = 1$. Fig. 4 shows the threshold ratio β_n in the case of a scaled-population phenotype mutation rate $\nu = 100 \gg 1$.

The biological intuition behind our results is that a high phenotype mutation rate reduces the number of interactions between cooperators and defectors because, in this case, groups are generally small and made of cooperators only or of defectors only, in which case the evolutionary process favors the strategy which has the higher payoff against itself, which is cooperation. On the contrary, a low phenotype mutation rate increases the occurrence of interactions between cooperators and defectors in large groups made of cooperators and defectors, in which selection opposes the evolution of cooperation (Antal et al., 2009c).

By contrast a low strategy mutation rate favors the evolution of cooperation. As a matter of fact the main effect of strategy mutation is to introduce mutant defectors which invade groups

of cooperators, and to introduce mutant cooperators which do not invade groups of defectors. The effect is stronger when the strategy mutation rate is higher.

Finally the effect of the dimension n of the phenotype space can be understood from the observation that if there is a group of cooperators with a given phenotype and there exists a defector in a group with an adjacent phenotype, then the probability of migration of this defector to the group of cooperators (given by $v/(2n)$), and therefore the probability of invasion of the group of cooperators by defectors, is a decreasing function with respect to the dimension n. As a result, it is easier for cooperation to evolve in a phenotype space of higher dimension because it becomes more difficult for a defector to migrate to a group of cooperators. The difference is significant from $n = 1$ to $n = 2$ and from $n = 2$ to $n = 3$, but becomes small as soon as $n \geq 3$. There might be a link between this phenomenon and the properties of symmetric random walks, which are recurrent for $n = 1$ or $n = 2$ but transient for $n \geq 3$ (Norris, 1997).

Acknowledgment

Appendix A. Existence of stationary state

In this section, we consider the neutral case when all players have the same fertility. Let $\underline{\mathbf{X}}_t = \left(\mathbf{X}_t(1), \ldots, \mathbf{X}_t(N) \right)$, where $\mathbf{X}_t(k)$ is the phenotype of individual k for $k = 1, \ldots, N$, in generation $t \geq 0$. The Markov chain $\underline{\mathbf{X}}_t$ for $t \geq 0$ is irreducible on the state space $(\mathbb{Z}^n)^N$. This can be seen from two observations. First, the diagonal

$$\Delta = \{(\mathbf{x}, \ldots, \mathbf{x}) : \mathbf{x} \in \mathbb{Z}^n\}$$

can be reached with positive probability in one generation from any state $\underline{\mathbf{x}} \in (\mathbb{Z}^n)^N$ by considering the scenario where all individuals in the next generation have the same parent. Conversely, any state $\underline{\mathbf{x}}$ can be reached from some state on the diagonal Δ in finitely many generations. This is a consequence of the fact that from a phenotype $\mathbf{x}$, the phenotype $\mathbf{x} + \mathbf{e}_i$ or $\mathbf{x} - \mathbf{e}_i$ can be reached in one generation with a positive probability $\frac{v}{2n}$, for any integer $i \in \{1, \ldots, n\}$. Then the phenotype $\mathbf{x} + l\mathbf{e}_i$ can be reached in $|l|$ generations for any integer $l \in \mathbb{Z}$, where $|l|$ is the absolute value of l. Secondly, any $\mathbf{y} \in \Delta$ can be reached from any $\underline{\mathbf{x}} \in \Delta$ in finitely many generations, by making all coordinates of $\underline{\mathbf{X}}_t$ move in the same direction in each generation. But $\underline{\mathbf{X}}_t$ for $t \geq 0$ cannot be positive recurrent because the process rapidly reaches a cluster and this cluster diffuses collectively through the phenotype space $(\mathbb{Z}^n)^N$ (see Antal et al., 2009c). For this reason we focus on differences in the phenotype space. Let us consider the associated Markov chain

$$\underline{\mathbf{D}}_t = \left(\mathbf{X}_t(1) - \mathbf{X}_t(N), \ldots, \mathbf{X}_t(N-1) - \mathbf{X}_t(N) \right),$$

for $t \geq 0$. This chain gives the differences between the phenotypes of individuals $1, \ldots, N-1$ and the phenotype of individual N. We are now interested in the transition probabilities of this Markov chain. Let

$$\mathbf{J} = \left\{ -\mathbf{e}_{n-1}, \ldots, -\mathbf{e}_1, \mathbf{0}, \mathbf{e}_1, \ldots, \mathbf{e}_{n-1} \right\},$$

where $\mathbf{e}_i \in \mathbb{Z}^n$ is a n-dimensional unit vector with 1 in the ith component, and 0 elsewhere, for $i = 1, \ldots, n-1$, and $\mathbf{0}$ is a n-dimensional zero vector. Let $|\sigma|$ be the norm of $\sigma \in \mathbf{J}$ defined by 1 if $\sigma = \pm\mathbf{e}_i$ for some $i = 1, \ldots, n-1$, and 0 if $\sigma = \mathbf{0}$. Assume that $\sigma_k \in \mathbf{J}$ describes how the phenotype of individual k is obtained from the phenotype of its parent. If $\sigma_k = \mathbf{0}$, then the phenotype of

k is the same as its parent's phenotype, which occurs with probability $1 - v$. If $\sigma_k = \mathbf{e}_i$ ($\sigma_k = -\mathbf{e}_i$ respectively), then the phenotype of k is obtained by increasing (decreasing respectively) by 1 the ith component of its parent's phenotype, which occurs with probability $\frac{v}{2n}$. For $\underline{\mathbf{d}} = \left(\mathbf{d}(1), \ldots, \mathbf{d}(N-1) \right) \in (\mathbb{Z}^n)^{N-1}$ and $\underline{\mathbf{b}} = \left(\mathbf{b}(1), \ldots, \mathbf{b}(N-1) \right) \in (\mathbb{Z}^n)^{N-1}$, the transition probability

$$P(\underline{\mathbf{d}}, \underline{\mathbf{b}}) = \mathbb{P}(\underline{\mathbf{D}}_{t+1} = \underline{\mathbf{b}} | \underline{\mathbf{D}}_t = \underline{\mathbf{d}})$$

is given by

$$P(\underline{\mathbf{d}}, \underline{\mathbf{b}}) = \sum_{\sigma_1, \ldots, \sigma_{N-1} \in \mathbf{J}} \prod_{k=1}^{N-1} \frac{\#\{l : \mathbf{d}(l) = \mathbf{b}(k) + \sigma_k\}}{N} \times \left((1 - |\sigma_k|)(1 - v) + |\sigma_k| \frac{v}{2n} \right). \tag{49}$$

Here, $\#\{l : \mathbf{d}(l) = \mathbf{b}(k) + \sigma_k\}$ is the number of choices for the parent of individual k given that the phenotype of k is obtained from the phenotype of its parent with a σ_k change. The probability of this σ_k change is $\left((1 - |\sigma_k|)(1 - v) + |\sigma_k| \frac{v}{2n} \right)$.

Lemma A.1. Let $\{Y_t : t \geq 0\}$ be an irreducible Markov chain on a countable state space E with transition matrix Q. Assume that there exist $x_0 \in E$ and $p > 0$ such that

$$Q(x, x_0) \geq p, \quad \text{for all } x \neq x_0. \tag{50}$$

Then $\{Y_t : t \geq 0\}$ is positive recurrent.

Proof. Let $Y_0 = x_0$ and define T_{x_0} as the time of the first return of Y_t to x_0, that is

$$T_{x_0} := \inf\{t \geq 1 : Y_t = x_0\}.$$

Note first that we have the inequality

$$\mathbb{P}\left(T_{x_0} \geq t \Big| Y_0 = x_0 \right) \leq (1 - p)^{t-1}, \tag{51}$$

for $t \geq 1$. As a matter of fact, we have

$$\mathbb{P}(Y_1 \neq x_0, \ldots, Y_t \neq x_0 | Y_0 = x_0)$$
$$= \sum_{y_1, \ldots, y_t \neq x_0} \mathbb{P}(Y_t = y_t, Y_{t-1} = y_{t-1}, \ldots, Y_1 = y_1 | Y_0 = x_0)$$
$$= \sum_{y_1, \ldots, y_{t-1} \neq x_0} \sum_{y_t \neq x_0} \mathbb{P}(Y_{t-1} = y_{t-1}, \ldots, Y_1 = y_1 | Y_0 = x_0)$$
$$\times (Y_t = y_t | Y_{t-1} = y_{t-1})$$
$$= \sum_{y_1, \ldots, y_{t-1} \neq x_0} \mathbb{P}(Y_{t-1} = y_{t-1}, \ldots, Y_1 = y_1 | Y_0 = x_0)\mathbb{P}$$
$$\times (1 - \mathbb{P}(Y_t = x_0 | Y_{t-1} = y_{t-1}))$$
$$\leq (1 - p)\mathbb{P}\left(Y_1 \neq x_0, \ldots, Y_{t-1} \neq x_0 \Big| Y_0 = x_0 \right),$$

owing to (50). The inequality (51) follows by recurrence. Now using the fact that

$$\{T_{x_0} = \infty\} = \bigcap_{t \geq 1} \{T_{x_0} \geq t\},$$

we obtain

$$\mathbb{P}\left(T_{x_0} = \infty \Big| Y_0 = x_0 \right) = \lim_{t \to \infty} \mathbb{P}\left(T_{x_0} \geq t \Big| Y_0 = x_0 \right)$$
$$\leq \lim_{t \to \infty} (1 - p)^{t-1} = 0.$$

Therefore, the state x_0 is recurrent. Turn now to the expected value of T_{x_0}. We have

$$\mathbb{E}\left[T_{x_0} \Big| Y_0 = x_0 \right] = \sum_{t=1}^{\infty} \mathbb{P}\left(T_{x_0} \geq t \Big| Y_0 = x_0 \right)$$

$$\le \sum_{t=1}^{\infty} (1-p)^{t-1} = \frac{1}{p} < \infty.$$

We conclude that x_0 is positive recurrent. Since the chain is irreducible, it is positive recurrent, which completes the proof. □

Proposition A.1. *If $N \ge 2$ and $v \in [0, 1]$, then the associated Markov chain $\underline{\mathbf{D}}_t$ for $t \ge 0$ is positive recurrent.*

Proof. Note first that $\underline{\mathbf{D}}_t$ for $t \ge 0$ is irreducible on the state space $(\mathbb{Z}^n)^{N-1}$ since $\underline{\mathbf{X}}_t$ for $t \ge 0$ is irreducible on the state space $(\mathbb{Z}^n)^N$. Fix a starting state $\underline{\mathbf{d}} \in (\mathbb{Z}^n)^{N-1}$. Note that the event $\{\underline{\mathbf{D}}_1 = \underline{\mathbf{0}}\}$ contains the union of the disjoint events Γ_i for $i = 1, \dots, N$, where Γ_i is the scenario when all individuals in generation 1 have the ith individual in generation 0 as their common parent, which occurs with probability $(\frac{1}{N})^N$. Moreover, they may all stay at the location of their common parent, with probability $(1-v)^N$, or all move to the same direction with probability $(\frac{v}{2n})^N$ (there are $2n$ possible directions). Hence,

$$
\begin{aligned}
P(\underline{\mathbf{d}}, \underline{\mathbf{0}}) &\ge \sum_{i=1}^{N} P(\Gamma_i) \\
&= \sum_{i=1}^{N} \frac{(1-v)^N + 2n(\frac{v}{2n})^N}{N^N} = \frac{(1-v)^N}{N^{N-1}} + \frac{v^N}{(2nN)^{N-1}} \\
&= p(v, n, N) > 0.
\end{aligned}
$$

By the previous lemma, we conclude that the chain is positive recurrent, and the proof is complete. □

Appendix B. Identity measures under neutrality

In this section, we derive the different identity measures y_n, z_n, g_n, h_n and η_n in the stationary state under neutrality ($\delta = 0$) in the limit of a large population ($N \to \infty$). We assume that the strategy mutation rate u_N and the phenotype mutation rate v_N depend on the population size N such as $\lim_{N\to\infty} Nv_N = \mu$ and $\lim_{N\to\infty} Nu_N = \nu$, where μ and ν are two positive constants. More precisely, we suppose that $u_N = \frac{\mu}{N}$ and $v_N = \frac{\nu}{N}$.

B.1. Ancestral process

The calculations in this section are based on properties of the ancestral process in the limit of a large population size which are well known in coalescent theory since Kingman (1982).

- Let $t_N(k, j)$ denote the time back to the most recent common ancestor (MRCA) in number of generations for two individuals k and j chosen at random in the same generation in a population of size N. The rescaled coalescence time taking N generations as unit of time $t_N(k, j)/N$ converges in distribution to a continuous random variable $\tau(k, j)$ as $N \to \infty$, whose density function is given by

$$f_1(\tau) = e^{-\tau}, \tag{52}$$

for $\tau > 0$.

Proof. The lineages of two individuals coalesce in each generation with probability $1/N$. Then, we have

$$\mathbb{P}_0\left(t_N(k, j) > t\right) = \left(1 - \frac{1}{N}\right)^t, \tag{53}$$

for any integer $t \ge 1$. Therefore,

$$\mathbb{P}_0\left(\frac{t_N(k, j)}{N} > \tau\right) = \left(1 - \frac{1}{N}\right)^{\lfloor N\tau \rfloor},$$

for any real number $\tau > 0$. Here $\lfloor . \rfloor$ denotes the integer part function. In the limit of a large population size, we get

$$\lim_{N\to\infty} \mathbb{P}_0\left(\frac{t_N(k, j)}{N} > \tau\right) = \lim_{N\to\infty} \left(1 - \frac{1}{N}\right)^{\lfloor N\tau \rfloor} = e^{-\tau},$$

for any real number $\tau > 0$. □

- Similarly, let $t_N^{(3)}(k, j, l)$ be the first coalescence time of two lineages in number of generations back among the lineages of three individuals k, j and l chosen at random in the same generation, and $t_N^{(2)}(k, j, l)$ be the supplementary time for the coalescence of the two remaining lineages. The rescaled coalescence time vector $\left(\frac{t_N^{(3)}(k,j,l)}{N}, \frac{t_N^{(2)}(k,j,l)}{N}\right)$ taking N generations as unit of time converges in distribution to a continuous random vector $\left(\tau^{(3)}(k, j, l), \tau^{(2)}(k, j, l)\right)$, whose joint density function is given by

$$f_2(\tau_3, \tau_2) = 3e^{-(3\tau_3 + \tau_2)}, \tag{54}$$

for $\tau_3, \tau_2 > 0$.

Proof. The probability of no coalescence event in one generation back among the ancestral lines of k, j and l is $\left(1 - \frac{1}{N}\right)\left(1 - \frac{2}{N}\right)$. The probability that two lines coalesce is $\frac{3}{N}\left(1 - \frac{1}{N}\right)$. The remaining two lines coalesce later on with probability $1/N$ in each generation backward in time. Then, the probability that the first coalescence event occurs at time back $t_N^{(3)}(k, j, l) > \lfloor N\tau_3 \rfloor$ in number of generations and the second at time back $t_N^{(2)}(k, j, l) > \lfloor N\tau_2 \rfloor$ in number of generations is

$$
\begin{aligned}
&\mathbb{P}_0\left(\frac{t_N^{(3)}(k, j, l)}{N} > \tau_3, \frac{t_N^{(2)}(k, j, l)}{N} > \tau_2\right) \\
&= \left[\left(1 - \frac{1}{N}\right)\left(1 - \frac{2}{N}\right)\right]^{\lfloor N\tau_3 \rfloor} \left(1 - \frac{1}{N}\right)^{\lfloor N\tau_2 \rfloor},
\end{aligned}
$$

for any real numbers $\tau_3, \tau_2 > 0$. Now using the limit

$$\lim_{N\to\infty} \left(1 + \frac{a}{N} + o(N^{-1})\right)^{\lfloor N\tau \rfloor} = e^{a\tau},$$

we obtain

$$\lim_{N\to\infty} \mathbb{P}_0\left(\frac{t_N^{(3)}(k, j, l)}{N} > \tau_3, \frac{t_N^{(2)}(k, j, l)}{N} > \tau_2\right) = e^{-(3\tau_3 + \tau_2)},$$

for any real numbers $\tau_3, \tau_2 > 0$. □

- Now, let S_τ^N (respectively L_τ^N) be the number of strategy mutations (respectively the number of phenotype mutations) on an ancestral line of length $\lfloor N\tau \rfloor$ in number of generations, which corresponds to a length τ with N generations as unit of time. Then, S_τ^N (respectively L_τ^N) converges in distribution to a Poisson variable of parameter $\mu\tau$ (respectively $\nu\tau$) as $N \to \infty$. Moreover, this variable is independent of the number of mutations on other disjoint ancestral lines.

Proof. Let S_τ^N be the number of strategy mutations on an ancestral line of length τ backward in time, taking N generations as unit of time. Then, we have

$$\mathbb{P}_0\left(S_\tau^N = L\right) = \binom{\lfloor N\tau \rfloor}{L} u_N^L (1 - u_N)^{\lfloor N\tau \rfloor - L}.$$

Here, $\binom{\lfloor N\tau \rfloor}{L}$ is the number of combinations of L generations among $\lfloor N\tau \rfloor$ along the ancestral line of length τ, while u_N^L is the probability of strategy mutation in all those generations and $(1 - u_N)^{\lfloor N\tau \rfloor - L}$ the probability of no strategy mutation in all the

other generations. This is the probability mass function of a binomial distribution with parameters $\lfloor N\tau \rfloor$ and u_N. In the limit of a large number of generations as unit of time, we get

$$\binom{\lfloor N\tau \rfloor}{L} u_N^L = \frac{\mu^L}{L!} \times \frac{\lfloor N\tau \rfloor}{N} \times \cdots \times \frac{\lfloor N\tau \rfloor - L + 1}{N}$$

$$= \frac{\mu^L \tau^L}{L!} + o(1),$$

since $\frac{\lfloor N\tau \rfloor}{N} = \tau + o(1)$ as $N \to \infty$. Here, $o(1)$ is a function of N such that

$$\lim_{N \to \infty} o(1) = 0.$$

Using the last result and the following limit

$$(1 - u_N)^{\lfloor N\tau \rfloor - L} = \left(1 - \frac{\mu}{N}\right)^{\lfloor N\tau \rfloor - L} = e^{-\mu\tau} + o(1),$$

we obtain

$$\lim_{N \to \infty} \mathbb{P}_0(S_\tau^N = L) = e^{-\mu\tau} \frac{(\mu\tau)^L}{L!},$$

for any real number $\tau > 0$. This is the probability mass function of a Poisson distribution with parameter $\mu\tau$. $\square$

B.2. Phenotypic similarity

First let us focus on the probability that two distinct individuals, k and j, chosen at random in the same generation of the population in the stationary state, have the same phenotype given that the time of coalescence of their lineages backward in time $\tau(k, j)$ in number of N generations as $N \to \infty$ equals $\tau > 0$. Let $\lambda(k, j)$ be the number of phenotype mutations on the ancestral lines of k and j back to their most recent common ancestor (MRCA). Then we have

$$\mathbb{P}_0\Big(\lambda(k, j) = L \,\Big|\, \tau(k, j) = \tau\Big) = e^{-2\nu\tau} \frac{(2\nu\tau)^L}{L!}, \tag{55}$$

for $\tau > 0$. This is the probability mass function for a Poisson distribution with parameter $2\nu\tau$.

Let h_i be the number of increases in the ith component of the phenotype (the number of changes $\mathbf{x} \to \mathbf{x} + \mathbf{e}_i$) on the ancestral lines of k and j back to the MRCA and b_i be the number of decreases in this component (the number of changes $\mathbf{x} \to \mathbf{x} - \mathbf{e}_i$, for $i = 1, \ldots, n$. Then, the difference between the phenotypes of individuals k and j is given by

$$\mathbf{x}(k) - \mathbf{x}(j) = (h_1 - b_1, \ldots, h_n - b_n).$$

Therefore, the two individuals have the same phenotype ($\mathbf{x}(k) = \mathbf{x}(j)$) if and only if $h_i = b_i$, for $i = 1, \ldots, n$. Then, the total number of phenotype mutations is

$$L = \sum_{i=1}^{n} (h_i + b_i) = 2L',$$

where

$$L' = \sum_{i=1}^{n} h_i.$$

On the other hand, given an even number of phenotype mutations, the conditional probability that k and j have the same phenotype is

$$\mathbb{P}_0\Big(\mathbf{x}(k) = \mathbf{x}(j) \,\Big|\, \lambda(k, j) = 2L'\Big)$$

$$= \sum_{\substack{0 \le h_1, \ldots, h_n \\ h_1 + \cdots + h_n = L'}} \binom{2L'}{h_1, h_1, \ldots, h_n, h_n} \left(\frac{1}{2n}\right)^{2L'}, \tag{56}$$

where $\binom{2L'}{h_1, h_1, \ldots, h_n, h_n}$ gives the number of choices for the positions of the increases and decreases among the $2L'$ phenotype mutations, and $\frac{1}{2n}$ is the probability that a given phenotype mutation is of a given type among $2n$ types, n types of increase and n types of decrease.

Let $\xi_n(\tau)$ be the probability that two individuals k and j have the same phenotype in the neutral model at stationarity given that the time of coalescence of their lineages backward in time in number of N generations as $N \to \infty$ is $\tau(k, j) = \tau > 0$. More precisely, we define

$$\xi_n(\tau) = \mathbb{P}_0\Big(\mathbf{x}(k) = \mathbf{x}(j) \,\Big|\, \tau(k, j) = \tau\Big).$$

Lemma B.1. *We have the expression*

$$\xi_n(\tau) = e^{-2\nu\tau} \sum_{L'=0}^{\infty} \sum_{\substack{0 \le h_1, \ldots, h_n \\ h_1 + \cdots + h_n = L'}} \frac{1}{(h_1!)^2 \times \cdots \times (h_n!)^2} \left(\frac{\nu\tau}{n}\right)^{2L'}, \tag{57}$$

for every integer $n \ge 1$.

Proof. Conditioning on the number of phenotype mutations on the ancestral lines of k and j, we have

$$\xi_n(\tau) = \sum_{L'=0}^{\infty} \mathbb{P}_0\Big(\mathbf{x}(k) = \mathbf{x}(j) \,\Big|\, \lambda(k, j) = 2L', \tau(k, j) = \tau\Big)$$

$$\times \mathbb{P}_0\Big(\lambda(k, j) = 2L' \,\Big|\, \tau(k, j) = \tau\Big).$$

Now using (55) and (56), we obtain

$$\xi_n(\tau) = \sum_{L'=0}^{\infty} \sum_{\substack{0 \le h_1, \ldots, h_n \\ h_1 + \cdots + h_n = L'}} \binom{2L'}{h_1, h_1, \ldots, h_n, h_n} \left(\frac{1}{2n}\right)^{2L'} e^{-2\nu\tau} \frac{(2\nu\tau)^{2L'}}{(2L')!}$$

$$= e^{-2\nu\tau} \sum_{L'=0}^{\infty} \sum_{\substack{0 \le h_1, \ldots, h_n \\ h_1 + \cdots + h_n = L'}} \frac{1}{(h_1!)^2 \times \cdots \times (h_n!)^2} \left(\frac{\nu\tau}{n}\right)^{2L'}.$$

This completes the proof. $\square$

Lemma B.2. *In terms of the Modified Bessel function of index 0, we have the recurrence formula*

$$\xi_n(\tau) = e^{-\frac{2\nu\tau}{n}} I_0\left(\frac{2\nu}{n}\tau\right) \xi_{n-1}\left(\frac{n-1}{n}\tau\right), \tag{58}$$

for every integer $n \ge 2$.

Proof. From (57) and (24), we have

$$e^{2\nu\tau} \xi_n(\tau) = \sum_{L=0}^{\infty} \sum_{\substack{0 \le h_1, \ldots, h_n \\ h_1 + \cdots + h_n = L}} \frac{1}{(h_1!)^2 \times \cdots \times (h_n!)^2} \left(\frac{\nu\tau}{n}\right)^{2L}$$

$$= \sum_{L=0}^{\infty} \sum_{h_n=0}^{L} \frac{1}{(h_n!)^2} \left(\frac{\nu\tau}{n}\right)^{2h_n}$$

$$\times \sum_{\substack{0 \le h_1, \dots, h_{n-1} \\ h_1 + \dots + h_{n-1} = L - h_n}} \frac{1}{(h_1!)^2 \times \dots \times (h_{n-1}!)^2} \left(\frac{\nu\tau}{n}\right)^{2(L-h_n)}$$

$$= \sum_{h_n=0}^{\infty} \frac{1}{(h_n!)^2} \left(\frac{\nu\tau}{n}\right)^{2h_n}$$

$$\times \sum_{L=h_n}^{\infty} \sum_{\substack{0 \le h_1, \dots, h_{n-1} \\ h_1 + \dots + h_{n-1} = L - h_n}} \frac{1}{(h_1!)^2 \times \dots \times (h_{n-1}!)^2} \left(\frac{\nu\tau}{n}\right)^{2(L-h_n)}$$

$$= \sum_{h_n=0}^{\infty} \frac{1}{(h_n!)^2} \left(\frac{\nu\tau}{n}\right)^{2h_n}$$

$$\times \sum_{L'=0}^{\infty} \sum_{\substack{0 \le h_1, \dots, h_{n-1} \\ h_1 + \dots + h_{n-1} = L'}} \frac{1}{(h_1!)^2 \times \dots \times (h_{n-1}!)^2} \left(\frac{\nu\tau}{n}\right)^{2L'}$$

$$= I_0\left(\frac{2\nu}{n}\tau\right) \sum_{L'=0}^{\infty} \sum_{\substack{0 \le h_1, \dots, h_{n-1} \\ h_1 + \dots + h_{n-1} = L'}} \frac{1}{(h_1!)^2 \times \dots \times (h_{n-1}!)^2}$$

$$\times \left(\frac{\nu\tau(n-1)}{n} \frac{1}{n-1}\right)^{2L'}$$

$$= e^{\frac{2\nu\tau(n-1)}{n}} I_0\left(\frac{2\nu}{n}\tau\right) \xi_{n-1}\left(\frac{n-1}{n}\tau\right).$$

Multiplying by $e^{-2\nu\tau}$ gives the stated result. $\quad\square$

Proposition B.1. *In terms of the Modified Bessel function of index 0, we have*

$$\xi_n(\tau) = e^{-2\nu\tau} \left(I_0\left(\frac{2\nu}{n}\tau\right)\right)^n, \tag{59}$$

for every integer $n \ge 1$.

Proof. We will show the result by recurrence. First, for $n = 1$, the expression (58) reduces to

$$\xi_1(\tau) = e^{-2\nu\tau} I_0(2\nu\tau) = e^{-2\nu\tau} \sum_{L=0}^{\infty} \frac{1}{(L!)^2} (\nu\tau)^{2L},$$

which holds owing to (57). Now, suppose that (58) holds for some integer $n \ge 1$. Then, owing to Lemma B.2, we have

$$\xi_{n+1}(\tau) = e^{-\frac{2\nu\tau}{n+1}} I_0\left(\frac{2\nu}{n+1}\tau\right) \xi_n\left(\frac{n}{n+1}\tau\right)$$

$$= e^{-\frac{2\nu\tau}{n+1}} I_0\left(\frac{2\nu}{n+1}\tau\right) e^{-2\nu\frac{n}{n+1}\tau} \left(I_0\left(\frac{2\nu}{n}\frac{n}{n+1}\tau\right)\right)^n$$

$$= e^{-2\nu\tau} \left(I_0\left(\frac{2\nu}{n+1}\tau\right)\right)^{n+1},$$

which means that (58) holds for $n+1$. This completes the proof. $\quad\square$

B.3. Identity measure y_n

We are interested in the calculation of the probability y_n that two individuals k and j, chosen at random in the population in the stationary state under neutrality, have the same strategy. In the continuous time limit as $N \to \infty$, the conditional probability that k and j have the same strategy, given that the coalescence time back to their most recent common ancestor (MRCA) is equal to $\tau > 0$, takes the form

$$y_n(\tau) = \mathbb{P}_0\left(S(k) = S(j) \mid \tau(k,j) = \tau\right)$$

$$= e^{-2\mu\tau} + \frac{1}{2}(1 - e^{-2\mu\tau}) = \frac{1 + e^{-2\mu\tau}}{2}. \tag{60}$$

As a matter of fact, k and j have the same strategy if there is no strategy mutation on their ancestral lines back to the MRCA, which occurs with probability $e^{-2\mu\tau}$. If there is at least one mutation, which occurs with the complementary probability $1 - e^{-2\mu\tau}$, then at least one of the two individuals has a random strategy, which is the same as the strategy of the other individual with probability $1/2$. Let us now calculate the probability y_n in the limit of a large population, by conditioning on the coalescence time $\tau(k,j)$ of k and j. We obtain

$$y_n = \mathbb{P}_0\left(S(k) = S(j)\right)$$

$$= \int_0^{\infty} \mathbb{P}_0\left(S(k) = S(j) \mid \tau(k,j) = \tau\right) f_1(\tau) d\tau$$

$$= \int_0^{\infty} y_n(\tau) f_1(\tau) d\tau. \tag{61}$$

Then, by using the expression (52) for $f_1(\tau)$ and the expression (60) for $y_n(\tau)$, we obtain

$$y_n = \int_0^{\infty} \frac{1 + e^{-2\mu\tau}}{2} \times e^{-\tau} d\tau = \frac{1 + \mu}{1 + 2\mu}. \tag{62}$$

B.4. Identity measure z_n

Let k and j be two different individuals from the population in the stationary state under neutrality. Similarly to the previous subsection, by conditioning on the coalescence time $\tau(k,j)$ of individuals k and j, we obtain

$$z_n = \mathbb{P}_0\left(\mathbf{x}(k) = \mathbf{x}(j)\right)$$

$$= \int_0^{\infty} \mathbb{P}_0\left(\mathbf{x}(k) = \mathbf{x}(j) \mid \tau(k,j) = \tau\right) f_1(\tau) d\tau$$

$$= \int_0^{\infty} \xi_n(\tau) f_1(\tau) d\tau.$$

Now, by using (59) and (52), we have

$$z_n = \frac{n}{2\nu} G_n\left(\frac{1}{2\nu}\right). \tag{63}$$

Here, G_n denotes the function defined by the following expression

$$G_n(x) = \int_0^{\infty} \left(I_0(\sigma)\right)^n e^{-n(1+x)\sigma} d\sigma.$$

B.5. Identity measure g_n

In this subsection, we are interested in the calculation of the probability g_n, which denotes the probability that two individuals k and j, randomly chosen in the population in the stationary state under neutrality, have the same phenotype and the same strategy. Similarly to the previous subsections, by conditioning on the coalescence time $\tau(k,j)$ of k and j, we have

$$g_n = \mathbb{P}_0\left(\mathbf{x}(k) = \mathbf{x}(j), S(k) = S(j)\right)$$

$$= \int_0^{\infty} \mathbb{P}_0\left(\mathbf{x}(k) = \mathbf{x}(j), S(k) = S(j) \mid \tau(k,j) = \tau\right) f_1(\tau) d\tau. \tag{64}$$

Note that strategy mutations and phenotype mutations on any ancestral line occur independently. Therefore, we obtain

$$\mathbb{P}_0\left(S(k) = S(j), \mathbf{x}(k) = \mathbf{x}(j) \mid \tau(k,j) = \tau\right)$$

$$= \mathbb{P}_0\left(S(k) = S(j) \mid \tau(k,j) = \tau\right) \times \mathbb{P}_0\left(\mathbf{x}(k) = \mathbf{x}(j) \mid \tau(k,j) = \tau\right)$$

$$= \xi_n(\tau) \times y_n(\tau).$$

Then, the expression (64) becomes

$$g_n = \int_0^\infty y_n(\tau)\xi_n(\tau)f_1(\tau)d\tau. \tag{65}$$

Substituting the expressions (52), (59) and (60) for $f_1(\tau)$, $\xi_n(\tau)$ and $y_n(\tau)$, respectively, gives

$$g_n = \int_0^\infty \frac{1 + e^{-2\mu\tau}}{2}\xi_n(\tau)e^{-\tau}d\tau$$

$$= \frac{n}{4\nu}\left\{G_n\left(\frac{1}{2\nu}\right) + G_n\left(\frac{2\mu+1}{2\nu}\right)\right\}. \tag{66}$$

B.6. Identity measure h_n

In this subsection, we study the probability h_n that three individuals k, j and l, chosen at random under neutrality, are such that k and j have the same phenotype, while j and l have the same strategy, that is

$$h_n = \mathbb{P}_0\Big(\mathbf{x}(k) = \mathbf{x}(j), S(j) = S(l)\Big).$$

By conditioning on the first coalescence event in the continuous time limit, we obtain

$$h_n = \frac{1}{3}\Big(h_n^{(1)} + h_n^{(2)} + h_n^{(3)}\Big), \tag{67}$$

where

$$h_n^{(1)} = \mathbb{P}_0\Big(\mathbf{x}(k) = \mathbf{x}(j), S(j) = S(l)\Big|k \text{ and } j \text{ coalesce first}\Big),$$

$$h_n^{(2)} = \mathbb{P}_0\Big(\mathbf{x}(k) = \mathbf{x}(j), S(j) = S(l)\Big|j \text{ and } l \text{ coalesce first}\Big),$$

$$h_n^{(3)} = \mathbb{P}_0\Big(\mathbf{x}(k) = \mathbf{x}(j), S(j) = S(l)\Big|k \text{ and } l \text{ coalesce first}\Big).$$

If k and j coalesce first, then they coalesce at time back $\tau(k,j) = \tau_3$ and they coalesce later on with l at time back $\tau(j,l) = \tau_3 + \tau_2$. In this case, we have

$$\mathbb{P}_0\Big(\mathbf{x}(k) = \mathbf{x}(j), S(j) = S(l)\Big|\tau(k,j) = \tau_3, \tau(j,l) = \tau_3 + \tau_2\Big)$$

$$= \mathbb{P}_0\Big(\mathbf{x}(k) = \mathbf{x}(j)\Big|\tau(k,j) = \tau_3\Big)$$

$$\times \mathbb{P}_0\Big(S(j) = S(l)\Big|\tau(j,l) = \tau_3 + \tau_2\Big)$$

$$= \xi_n(\tau_3) \times y_n(\tau_3 + \tau_2).$$

Therefore, by conditioning on $(\tau_3(k,j,l), \tau_2(k,j,l)) = (\tau_3, \tau_2)$, we obtain

$$h_n^{(1)} = \int_0^\infty \int_0^\infty f_2(\tau_3, \tau_2)\xi_n(\tau_3)y_n(\tau_3 + \tau_2)d\tau_3 d\tau_2.$$

Similarly, if j and l coalesce first, then they coalesce at time back $\tau(j,l) = \tau_3$ and they coalesce later on with k at time back $\tau(k,j) = \tau_3 + \tau_2$. If, however k and l coalesce first, then we obtain $\tau(k,j) = \tau(j,l) = \tau_3 + \tau_2$. Therefore, conditioning on $(\tau_3(k,j,l), \tau_2(k,j,l)) = (\tau_3, \tau_2)$ gives

$$h_n^{(2)} = \int_0^\infty \int_0^\infty f_2(\tau_3, \tau_2)\xi_n(\tau_3 + \tau_2)y_n(\tau_3)d\tau_3 d\tau_2,$$

$$h_n^{(3)} = \int_0^\infty \int_0^\infty f_2(\tau_3, \tau_2)\xi_n(\tau_3 + \tau_2)y_n(\tau_3 + \tau_2)d\tau_3 d\tau_2.$$

Now using (54), (59), (60), we obtain

$$h_n^{(1)} = \int_0^\infty \left(\int_0^\infty 3e^{-(3\tau_3 + \tau_2)}\xi_n(\tau_3)\frac{1 + e^{-2\mu(\tau_2 + \tau_3)}}{2}d\tau_2\right)d\tau_3$$

$$= \frac{3}{2}\int_0^\infty \xi_n(\tau_3)\left(e^{-3\tau_3} + \frac{1}{1+2\mu}e^{-(3+2\mu)\tau_3}\right)d\tau_3$$

$$= \frac{3n}{4\nu}\left\{G_n\left(\frac{3}{2\nu}\right) + \frac{1}{1+2\mu}G_n\left(\frac{3+2\mu}{2\nu}\right)\right\},$$

$$h_n^{(2)} = \int_0^\infty \xi_n(\tau_4)\left(\int_0^{\tau_4} f_2(\tau_3, \tau_4 - \tau_3)y_n(\tau_3)d\tau_3\right)d\tau_4$$

$$= \int_0^\infty \xi_n(\tau_4)\left(\int_0^{\tau_4} 3e^{-(2\tau_3 + \tau_4)}\frac{1 + e^{-2\mu\tau_3}}{2}d\tau_3\right)d\tau_4$$

$$= \frac{3}{4}\int_0^\infty \xi_n(\tau_4)\left(\frac{2+\mu}{1+\mu}e^{-\tau_4} - e^{-3\tau_4} - \frac{1}{1+\mu}e^{-(3+2\mu)\tau_4}\right)d\tau_4$$

$$= \frac{3n}{8\nu}\left\{\frac{2+\mu}{1+\mu}G_n\left(\frac{1}{2\nu}\right) - G_n\left(\frac{3}{2\nu}\right) - \frac{1}{1+\mu}G_n\left(\frac{3+2\mu}{2\nu}\right)\right\}$$

and

$$h_n^{(3)} = \int_0^\infty \xi_n(\tau_4)y_n(\tau_4)\left(\int_0^{\tau_4} f_2(\tau_3, \tau_4 - \tau_3)d\tau_3\right)d\tau_4$$

$$= \int_0^\infty \xi_n(\tau_4)\frac{1 + e^{-2\mu\tau_4}}{2}\left(\int_0^{\tau_4} 3e^{-(2\tau_3 + \tau_4)}d\tau_3\right)d\tau_4$$

$$= \frac{3}{4}\int_0^\infty \xi_n(\tau_4)\left(e^{-\tau_4} + e^{-(2\mu+1)\tau_4} - e^{-3\tau_4} - e^{-(3+2\mu)\tau_4}\right)d\tau_4$$

$$= \frac{3n}{8\nu}\left\{G_n\left(\frac{1}{2\nu}\right) + G_n\left(\frac{1+2\mu}{2\nu}\right) - G_n\left(\frac{3}{2\nu}\right) - G_n\left(\frac{3+2\mu}{2\nu}\right)\right\}.$$

Finally, the identity measure given in (67) can be expressed as

$$h_n = \frac{n}{8\nu}\left\{\frac{3+2\mu}{1+\mu}G_n\left(\frac{1}{2\nu}\right) + G_n\left(\frac{1+2\mu}{2\nu}\right)\right.$$

$$\left. - \frac{\mu(3+2\mu)}{(1+\mu)(1+2\mu)}G_n\left(\frac{3+2\mu}{2\nu}\right)\right\}. \tag{68}$$

B.7. Identity measure η_n

First, we are interested in the probability, denoted by $y_n(\tau_3, \tau_2)$, that three individuals k, j and l, randomly chosen in the population in the stationary state under neutrality, have the same strategy, given that two of them coalesce first at time back $\tau_3 > 0$ and coalesce later on with the third at time back $\tau_2 + \tau_3 > 0$ in the continuous time limit. Without loss of generality, we suppose that k and j coalesce first. The individuals k, j and l have the same strategy in two cases. In the first case, the most recent common ancestor of k and j, say m, does not have the same strategy as l, which occurs with probability $\frac{1-e^{-\mu(2\tau_2 + \tau_3)}}{2}$. This is $1/2$ times the probability of at least one mutation event on the ancestral lines of m and l back to their most recent common ancestor. In this case, there must be mutation events on the ancestral line of k and on the ancestral line of j back to their most recent common ancestor, which occurs with probability $(1 - e^{-\mu\tau_3})^2$. Moreover, following the last mutation event on each of the two lines, the strategy chosen in both cases must be that of l, which occurs with probability $1/4$. In the second case, the most recent common ancestor of k and j, say m, has the same strategy as l, which occurs with probability $\frac{1+e^{-\mu(2\tau_2 + \tau_3)}}{2}$. In this case, the individuals k and j have the same strategy as l if k and m (j and m respectively) have the same strategy, which occurs with probability $\frac{1+e^{-\mu\tau_3}}{2}$ ($\frac{1+e^{-\mu\tau_3}}{2}$ respectively). Then, we obtain

$$y_n(\tau_3, \tau_2) = \frac{1 - e^{-\mu(2\tau_2 + \tau_3)}}{2}\left(\frac{1 - e^{-\mu\tau_3}}{2}\right)^2$$

$$+ \frac{1 + e^{-\mu(2\tau_2 + \tau_3)}}{2}\left(\frac{1 + e^{-\mu\tau_3}}{2}\right)^2$$

$$= \frac{1}{4}\Big(1 + e^{-2\mu\tau_3} + 2e^{-2\mu(\tau_2 + \tau_3)}\Big). \tag{69}$$

Now, let η_n be the probability that three individuals k, j and l, chosen at random in the population in the stationary state under neutrality, have the same strategy and k and j have the same phenotype, that is

$$\eta_n = \mathbb{P}_0\Big(\mathbf{x}(k) = \mathbf{x}(j), S(k) = S(j) = S(l)\Big).$$

As previously, we condition on the first coalescence event in the continuous time limit. If k and j coalesce first, which occurs with probability 1/3, then they coalesce at time back $\tau(k, j) = \tau_3$ and they coalesce later on with l at time back $\tau(j, l) = \tau_3 + \tau_2$. In this case, we have

$$\mathbb{P}_0\Big(\mathbf{x}(k) = \mathbf{x}(j), S(k) = S(j) = S(l)\Big|\tau(k, j) = \tau_3, \tau(j, l) = \tau_3 + \tau_2\Big)$$
$$= \mathbb{P}_0\Big(\mathbf{x}(k) = \mathbf{x}(j)\Big|\tau(k, j) = \tau_3, \tau(j, l) = \tau_3 + \tau_2\Big)$$
$$\times \mathbb{P}_0\Big(S(k) = S(j) = S(l)\Big|\tau(k, j) = \tau_3, \tau(j, l) = \tau_3 + \tau_2\Big)$$
$$= \xi_n(\tau_3) \times y_n(\tau_3, \tau_2).$$

However, if j and l (k and l respectively) coalesce first, which occurs with probability 1/3, then they coalesce at time back $\tau(j, l) = \tau_3$ ($\tau(k, l) = \tau_3$ respectively) and they coalesce later on with k (j respectively) at time back $\tau(k, j) = \tau_3 + \tau_2$ ($\tau(k, j) = \tau_3 + \tau_2$ respectively). Then, we have

$$\mathbb{P}_0\Big(\mathbf{x}(k) = \mathbf{x}(j), S(k) = S(j) = S(l)\Big|\tau(j, l) = \tau_3, \tau(k, j) = \tau_3 + \tau_2\Big)$$
$$= \mathbb{P}_0\Big(\mathbf{x}(k) = \mathbf{x}(j)\Big|\tau(j, l) = \tau_3, \tau(k, j) = \tau_3 + \tau_2\Big)$$
$$\times \mathbb{P}_0\Big(S(k) = S(j) = S(l)\Big|\tau(j, l) = \tau_3, \tau(k, j) = \tau_3 + \tau_2\Big)$$
$$= \xi_n(\tau_3 + \tau_2) \times y_n(\tau_3, \tau_2)$$

and

$$\mathbb{P}_0\Big(\mathbf{x}(k) = \mathbf{x}(j), S(k) = S(j) = S(l)\Big|\tau(k, l) = \tau_3, \tau(k, j) = \tau_3 + \tau_2\Big)$$
$$= \mathbb{P}_0\Big(\mathbf{x}(k) = \mathbf{x}(j)\Big|\tau(k, l) = \tau_3, \tau(k, j) = \tau_3 + \tau_2\Big)$$
$$\times \mathbb{P}_0\Big(S(k) = S(j) = S(l)\Big|\tau(k, l) = \tau_3, \tau(k, j) = \tau_3 + \tau_2\Big)$$
$$= \xi_n(\tau_3 + \tau_2) \times y_n(\tau_3, \tau_2).$$

Now, conditioning on $(\tau_3(k, j, l), \tau_2(k, j, l)) = (\tau_3, \tau_2)$ gives

$$\eta_n = \frac{1}{3}\Big(\eta_n^{(1)} + 2\eta_n^{(2)}\Big),\tag{70}$$

where

$$\eta_n^{(1)} = \mathbb{P}_0\Big(\mathbf{x}(k) = \mathbf{x}(j), S(j) = S(l)\Big|k \text{ and } j \text{ coalesce first}\Big)$$
$$= \int_0^\infty \int_0^\infty f_2(\tau_3, \tau_2)\xi_n(\tau_3)y_n(\tau_3, \tau_2)d\tau_3 d\tau_2$$

and

$$\eta_n^{(2)} = \mathbb{P}_0\Big(\mathbf{x}(k) = \mathbf{x}(j), S(j) = S(l)\Big|k \text{ and } j \text{ do not coalesce first}\Big)$$
$$= \int_0^\infty \int_0^\infty f_2(\tau_3, \tau_2)\xi_n(\tau_3 + \tau_2)y_n(\tau_3, \tau_2)d\tau_3 d\tau_2.$$

Substituting the expressions (54), (59) and (69) for $f_2(\tau)$, $\xi_n(\tau)$ and $y_n(\tau_3, \tau_2)$ respectively, gives

$$\eta_n^{(1)} = \int_0^\infty \Big(\int_0^\infty 3e^{-(3\tau_3+\tau_2)}\xi_n(\tau_3)\frac{1 + e^{-2\mu\tau_3} + 2e^{-2\mu(\tau_2+\tau_3)}}{4}d\tau_2\Big)d\tau_3$$
$$= \frac{3}{4}\int_0^\infty \xi_n(\tau_3)\Big(e^{-3\tau_3} + \frac{3+2\mu}{1+2\mu}e^{-(3+2\mu)\tau_3}\Big)d\tau_3$$
$$= \frac{3n}{8\nu}\Big\{G_n\Big(\frac{3}{2\nu}\Big) + \frac{3+2\mu}{1+2\mu}G_n\Big(\frac{3+2\mu}{2\nu}\Big)\Big\}$$

and

$$\eta_n^{(2)} = \int_0^\infty \xi_n(\tau_4)\Big(\int_0^{\tau_4} f_2(\tau_3, \tau_4 - \tau_3)y_n(\tau_3, \tau_4 - \tau_3)d\tau_3\Big)d\tau_4$$
$$= \int_0^\infty \xi_n(\tau_4)\Big(\int_0^{\tau_4} 3e^{-(2\tau_3+\tau_4)}\frac{1 + e^{-2\mu\tau_3} + 2e^{-2\mu\tau_4}}{4}d\tau_3\Big)d\tau_4$$
$$= \frac{3}{8}\int_0^\infty \xi_n(\tau_4)\Big(\frac{2+\mu}{1+\mu}e^{-\tau_4} + 2e^{-(1+2\mu)\tau_4}$$
$$- e^{-3\tau_4} - \frac{3+2\mu}{1+\mu}e^{-(3+2\mu)\tau_4}\Big)d\tau_4$$
$$= \frac{3n}{16\nu}\Big\{\frac{2+\mu}{1+\mu}G_n\Big(\frac{1}{2\nu}\Big) + 2G_n\Big(\frac{1+2\mu}{2\nu}\Big)$$
$$- \frac{3+2\mu}{1+\mu}G_n\Big(\frac{3+2\mu}{2\nu}\Big) - G_n\Big(\frac{3}{2\nu}\Big)\Big\}.$$

Plugging these expressions in Eq. (70) yields

$$\eta_n = \frac{n}{8\nu}\Big\{\frac{2+\mu}{1+\mu}G_n\Big(\frac{1}{2\nu}\Big) + 2G_n\Big(\frac{1+2\mu}{2\nu}\Big)$$
$$- \frac{\mu(3+2\mu)}{(1+\mu)(1+2\mu)}G_n\Big(\frac{3+2\mu}{2\nu}\Big)\Big\}.\tag{71}$$

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