

# Local Replicator Dynamics: A Simple Link Between Deterministic and Stochastic Models of Evolutionary Game Theory

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**Abstract** Classical replicator dynamics assumes that individuals play their games and adopt new strategies on a global level: Each player interacts with a representative sample of the population and if a strategy yields a payoff above the average, then it is expected to spread. In this article, we connect evolutionary models for infinite and finite populations: While the population itself is infinite, interactions and reproduction occurs in random groups of size  $N$ . Surprisingly, the resulting dynamics simplifies to the traditional replicator system with a slightly modified payoff matrix. The qualitative results, however, mirror the findings for finite populations, in which strategies are selected according to a probabilistic Moran process. In particular, we derive a one-third law that holds for any population size. In this way, we show that the deterministic replicator equation in an infinite population can be used to study the Moran process in a finite population and vice versa. We apply the results to three examples to shed light on the evolution of cooperation in the iterated prisoner's dilemma, on risk aversion in coordination games and on the maintenance of dominated strategies.

**Keywords** Evolutionary game theory · Replicator dynamics · Moran process · One-third rule · Evolution of cooperation

## 1 Introduction

Evolutionary game theory is the appropriate mathematical framework whenever the fitness of an individual does not only depend on its own phenotype but also on the composition of the whole population (Maynard Smith 1982; Nowak and Sigmund 2004). Such biological interdependencies are wide-spread. Game theoretic models help us to understand molecular biological processes (Pfeiffer and Schuster 2005),

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animal behaviour (Dugatkin and Reeve 1998) or plant growth (Falster and Westoby 2003). Even the evolution of abstract cultural entities, such as languages (Niyogi 2006) or norms (Gintis et al. 2005) can be captured with equations. In this way, mathematical arguments reveal the logic of indirect speech (Pinker et al. 2008) as well as the origin of moral systems (Uchida and Sigmund 2010).

The classical approach to evolutionary games is replicator dynamics (Taylor and Jonker 1978; Hofbauer and Sigmund 1998): When a certain strategy leads to a fitness above the average, then this behaviour is expected to spread. More formally, suppose the individuals of a population can choose among  $n$  strategies. A player with strategy  $i$ , interacting with a  $j$ -player, obtains a payoff  $a_{ij}$ . The relative frequency of  $i$ -individuals within the population is denoted by  $x_i$ . If we collect these frequencies to a vector  $x = (x_1, \dots, x_n)^T$  and the payoffs to a matrix  $A = (a_{ij})$ , the expected fitness of strategy  $i$  can be written as  $\pi_i(x) := (Ax)_i = a_{i1}x_1 + \dots + a_{in}x_n$ . Over the whole population, this results in an average payoff of  $\bar{\pi}(x) := x \cdot Ax$ . According to the replicator equation, the fraction of  $i$ -players grows whenever  $\pi_i(x)$  exceeds  $\bar{\pi}(x)$ :

$$\dot{x}_i = x_i \cdot [(Ax)_i - x \cdot Ax]. \quad (1)$$

The dot above  $x_i$  on the left-hand side denotes the time derivative,  $dx_i/dt$ .

There are several reasons for the prominent role of replicator dynamics: Firstly, (1) is relatively simple and mathematically well understood (Hofbauer and Sigmund 2003). It is equivalent to the famous Lotka–Volterra model in population ecology (Hofbauer 1981). Additionally, there are beautiful connections between replicator dynamics and the concepts of classical game theory (Fudenberg and Tirole 1991; Weibull 1995). For example, if strategy  $i$  is *dominated*, meaning that there is another strategy which is always better, then replicator dynamics will lead to the extinction of  $i$ . Furthermore, *strict Nash equilibria*, i.e. strategies that are optimal against themselves, are asymptotically stable rest points of (1).

The conceptual beauty of replicator dynamics has its price. To be valid, several conditions have to be met:

- (i) The population is *well mixed*, meaning that any two players interact with the same probability.
- (ii) Before reproduction, individuals play against a representative sample of the population.
- (iii) Players may choose among a finite set of strategies, and
- (iv) the population needs to be infinite.

The game-theoretical toolbox, however, is evolving, also. In the last two decades, there have been several attempts to relax the above assumptions. Instead of considering well mixed populations, various models explore games in which players only interact with their neighbors on a lattice (Nowak and May 1992; Durrett and Levin 1994; Hauert and Doebeli 2004; Helbing and Yu 2009) or on a random graph (Abramson and Kuperman 2001; Lieberman et al. 2005; Ohtsuki et al. 2006; Lehmann et al. 2007; Szabó and Fátih 2007; Santos et al. 2008). Additionally, some authors investigated the effect of a non-representative sample of interaction partners (Sánchez and Cuesta 2005; Roca et al. 2006; Traulsen et al. 2007; Wölfling and Traulsen 2009). The introduction of continuous strategy spaces has

led to adaptive dynamics theory (Hofbauer and Sigmund 1994; Geritz et al. 1998; Dieckmann et al. 2006).

To study the effect of finite populations, Nowak et al. (2004) consider a group of  $N$  individuals who may choose among two strategies,  $R$  and  $M$ . Evolution takes place according to a Moran process: In each time step, one randomly chosen individual dies. Its place is filled with the copy of another member of the population, whereby players with a high payoff have a better chance to be copied. The resulting dynamics is a stochastic birth-death process. Evolutionary success is measured with fixation probabilities. For example, in a state with  $R$ -types only, one may calculate the likelihood that one  $M$ -mutant can invade and take over the whole population. If this probability  $\rho_{M \rightarrow R}$  exceeds  $1/N$ , then *selection favours  $M$  replacing  $R$* .

There are interesting connections between replicator dynamics and the Moran-process. For example, in the limit of large populations, the diffusion approximation of the Moran-process converges to a variant of the replicator equation (Traulsen et al. 2005). A more subtle connection is called the one-third law (Taylor et al. 2004; Ohtsuki et al. 2007a; Bomze and Pawlowitsch 2008): Consider a game with payoff matrix

$$\begin{array}{c|cc} & R & M \\ \hline R & a & b \\ \hline M & c & d \end{array} \quad (2)$$

For  $a > c$  and  $d > b$ , replicator dynamics predicts that both pure strategies,  $R$  and  $M$ , are evolutionarily stable. Additionally, there is an interior fixed point at  $x^* = (a - c)/(a - b - c + d)$ , whereby  $x$  denotes the frequency of  $M$ -players. For large population sizes  $N$ , it can be shown that selection favours  $M$  replacing  $R$  if this fixed point is below one third, i.e.

$$\rho_{M \rightarrow R} > 1/N \Leftrightarrow x^* < 1/3. \quad (3)$$

A similar result holds for *risk dominance* (Harsanyi and Selten 1988): Strategy  $M$  has the bigger basin of attraction if  $M$  has a higher chance to replace  $R$  than vice versa:

$$\rho_{M \rightarrow R} > \rho_{R \rightarrow M} \Leftrightarrow x^* < 1/2. \quad (4)$$

Even if replicator dynamics and the Moran process are closely related for large populations, they can lead to very different conclusions if the population size  $N$  is small. Dominated strategies may spread in finite populations (Taylor et al. 2004) and regimes that are stable according to replicator dynamics may be invaded under the Moran process and vice versa (Nowak et al. 2004). Therefore, several recent studies have compared the dynamics in finite respectively infinite populations separately, e.g. Imhof et al. (2005) or Hilbe and Sigmund (2010).

In this paper, we aim to connect both approaches: While the population itself is infinite, individuals interact in randomly formed groups of size  $N$ . In each group, one member may adopt the strategy of a co-player. Strategies that yield a high payoff are more likely to be adopted. After reproduction, groups are formed anew. This scenario was used by Nakamaru et al. (1997, 1998), Nakamaru and Iwasa (2006) and Rand et al. (2010) to approximate games on a lattice, in which each player interacts with

its  $N - 1$  neighbors. Here, we show that the resulting dynamics can be described by a modified replicator equation. Instead of payoff matrix  $A$ , the modified matrix  $\tilde{A}_N = A - (A + A^T)/N$  governs the evolutionary outcome. We refer to this modified system as the *local replicator dynamics*.

Despite its deterministic nature, the local replicator dynamics strongly mirrors the findings for finite populations. We will show that there is a one-to-one map from the fixation probabilities according to the Moran process to the fixed points of the local replicator equation. In particular, the one-third rule holds for any population size  $N$ . Thus, a simple transformation of the payoff matrix allows us to use classical replicator dynamics to analyze games in finite populations.

The remainder of this article is organized as follows: In Sect. 2, we derive the local replicator equation, and in Sect. 3 we discuss its properties. In Sect. 4, we present three examples for the resulting dynamics: First, we show how the evolution of cooperation in the iterated prisoner's dilemma is influenced by the size of the group. Then we provide a simple model for the emergence of risk aversion in a coordination game. In the last example, we explain how dominated strategies can succeed in finite interaction neighborhoods. In Sect. 5, we extend our model: Instead of considering a fixed  $N$ , we assume that the size of a given group is a random variable. Still, the dynamics can be described with the local replicator equation by simply replacing  $N$  with a proper mean of all possible group sizes. In Sect. 6, finally, we give a summary and discussion of our results.

## 2 Derivation of the Local Replicator Dynamics

We consider an infinite population whose individuals are randomly assigned to groups of equal size. Within their groups, players engage in pairwise interactions that determine the payoff of each individual. More specifically, let  $k$  be the number of possible strategies and  $A = (a_{ij})$  the payoff matrix. For a given group of size  $N$ , denote by  $n_i$  the number of players with strategy  $i$  and by  $\vec{n} = (n_1, \dots, n_k)$  the vector of those numbers, with  $|\vec{n}| := n_1 + \dots + n_k = N$ . If individuals interact with every other group member and self-interactions are excluded, an individual with strategy  $i$  yields the average payoff

$$\pi_i(\vec{n}) = \frac{1}{N-1} [n_1 a_{i1} + \dots + (n_i - 1) a_{ii} + \dots + n_k a_{ik}].$$

After these interactions, one group member is chosen at random to compare its payoff with another randomly chosen group member. We follow the update rule in Traulsen et al. (2005, 2006) and assume that an  $i$ -player adopts the role model's strategy  $j$  with probability

$$p_{ij} = \frac{1}{2} + \frac{s}{2} \frac{\pi_j(\vec{n}) - \pi_i(\vec{n})}{\Delta\pi_{\max}},$$

where  $\Delta\pi_{\max}$  is the maximum possible payoff difference and  $0 < s \leq 1$  measures the strength of selection. For weak selection ( $s \approx 0$ ), a coin toss essentially determines

whether the role model is imitated; if the selection parameter approaches 1, this decision is increasingly biased towards the strategy with higher payoff. Since players are selected randomly for the imitation process, this leads to an expected change in the number of  $i$ -players of

$$\Delta n_i = \sum_{j=1}^k \frac{n_i}{N} \frac{n_j}{N} (p_{ji} - p_{ij}) = \frac{s}{\Delta\pi_{\max}} \frac{n_i}{N} [\pi_i(\vec{n}) - \bar{\pi}(\vec{n})]. \tag{5}$$

The term  $\bar{\pi}(\vec{n})$  denotes the average payoff of all players in the group,  $\bar{\pi}(\vec{n}) = \sum_{j=1}^k n_j \pi_j(\vec{n})/N$ . By using  $n_j/N$  instead of  $n_j/(N - 1)$ , we have implicitly assumed that players may imitate themselves (as, for example, in Ohtsuki et al. 2006; Ohtsuki and Nowak 2006). However, if an individual chooses itself as role model, then nothing will change. Overall, this simplification only changes the velocity of evolution but not its direction.

According to (5), the expected change of strategies within a certain group can be described through a replicator equation with local frequencies  $n_i/N$ . In order to calculate the aggregate outcome, we have to sum up over all possible groups with  $|\vec{n}| = N$ . If  $x_i$  denotes the global frequency of strategy  $i$  and if groups are formed according to a multi-nomial distribution, this results in the following equation for the expected change of global strategy abundances,

$$\dot{x}_i = \sum_{|\vec{n}|=N} \frac{N!}{n_1! \dots n_k!} x_1^{n_1} \dots x_k^{n_k} \cdot \frac{n_i}{N} [\pi_i(\vec{n}) - \bar{\pi}(\vec{n})], \tag{6}$$

where the constant factor  $s/\Delta\pi_{\max}$  has been omitted since it only affects the timescale of evolution. We call (6) the local replicator dynamics of the system. In general, the expression on the right-hand side is laborious to compute: The polynomial has degree  $N$  and the number of summands increases exponentially in the number of strategies  $k$ . As it turns out, this expression can be simplified considerably.

**Proposition 1** (A simple representation for the local replicator dynamics) *The local replicator dynamics (6) can be rewritten as*

$$\dot{x}_i = x_i \cdot [(\tilde{A}x)_i - x \cdot \tilde{A}x], \tag{7}$$

with  $\tilde{A} := A - \frac{A+A^T}{N}$ . As usual,  $A^T$  denotes the transposed payoff matrix (Proof in Appendix).

This representation of the local replicator equation can be interpreted by slightly rearranging the terms to

$$\dot{x}_i = x_i \cdot \left[ (Ax)_i - \frac{(N - 2) \cdot x^T Ax + (Ax)_i + (A^T x)_i}{N} \right],$$

meaning that a player with strategy  $i$  still gets an expected payoff of  $(Ax)_i$ . However, being an  $i$ -player in a finite group of size  $N$  leads to a bias in the average payoff of

the group, on the one hand due to the own payoff  $(Ax)_i$  and on the other hand due to the expected influence on the others' payoffs  $(A^T x)_i$ .

Consequently, there are two alternative mechanisms that promote the evolution of a certain strategy under the local replicator dynamics: Strategy  $i$  may spread either because it leads to a high own payoff  $(Ax)_i$ , or because it leads the co-players to have a low payoff, i.e. it decreases  $(A^T x)_i$ . In particular, it may pay off to be spiteful and to diminish the fitness of other group members (see also Nowak et al. 2004). As group size increases, the impact of spiteful behaviour disappears, since the own influence on the co-players' payoffs becomes negligible. In the limit of infinite group sizes, spite becomes completely irrelevant.

In this section, we have derived the local replicator dynamics for an imitation process, where individuals with higher payoff are imitated more often than others. One could also investigate a model in which successful players produce more offspring; such an attempt is shown in the appendix, leading to the same dynamics. Irrespective of its derivation, the local replicator equation has interesting properties: It connects the results of the Moran process in finite populations with the classical replicator dynamics in infinite populations. This is shown in the next section.

### 3 Properties of the Local Replicator Dynamics

Representation (7) makes it straightforward to derive the properties of the local replicator dynamics: We only have to plug in the values of  $A_N = A - (A + A^T)/N$ , to transfer the well-known results of the classical replicator equation (see, for example, in Hofbauer and Sigmund 1998). This is done in the following two propositions.

**Proposition 2** (Analytical properties of the local replicator equation)

1. *The simplex  $S_k = \{(x_1, \dots, x_k): x_1 + \dots + x_k = 1\}$  and all its sub-faces are invariant under the local replicator dynamics.*
2. *Quotient rule:  $\left(\frac{\dot{x}_i}{x_j}\right) = \frac{x_i}{x_j} \cdot \left[ (N - 1) \frac{(Ax)_i - (Ax)_j}{N} + \frac{(A^T x)_j - (A^T x)_i}{N} \right]$*
3. *In the special case of  $N = 2$ , the values of the diagonal entries of  $A$  do not influence the dynamics.*
4. *For zero sum games (i.e. if  $A = -A^T$ ) or in the case of infinite group sizes ( $N \rightarrow \infty$ ), the local replicator equation coincides with the classical version.*

In applications, it is often important to know which states can be stably established. To this end, one considers a homogeneous population with strategy  $R$ , that is invaded by a rare mutant with an alternative strategy  $M$ . If the evolutionary dynamics leads to the extinction of any such mutant, then  $R$  is called *evolutionarily stable* or an *ESS*.

**Proposition 3** (Evolutionary stability) *Consider a game with 2 strategies and payoff matrix*

$$\begin{array}{c|cc} & R & M \\ \hline R & a & b \\ \hline M & c & d \end{array}$$

Let  $x$  denote the fraction of  $M$ -players in the population. Then the local replicator dynamics can be written as

$$\dot{x} = x(1 - x) \cdot \left( \frac{(N - 1)c - b - (N - 2)a}{N} + \frac{(N - 2)(a - b - c + d)}{N} x \right).$$

In particular, the resident strategy  $R$  is (strictly) evolutionarily stable, if  $(N - 2)a + b > (N - 1)c$ .

Again, this proposition is simply an adapted version of the analogous result for classical replicator dynamics. Obviously, the above ESS-condition reduces to the usual Nash condition  $a > c$  for infinite groups. For finite populations, however, several definitions have been suggested to capture evolutionary stability, see Wild and Taylor (2004). The condition  $(N - 2)a + b > (N - 1)c$  is included, for example, in the definitions of Maynard Smith (1988) and Schaffer (1988).

Nowak et al. (2004) suggest an additional ESS-criterion for finite populations. Beside the above condition that rare mutants have a lower fitness than the resident type, they require the mutant strategy to have a fixation probability lower than  $1/N$ . When selection is weak (i.e. the impact of the payoff in the game has a small effect on the reproductive success of a strategy), they find that this fixation probability is approximately given by

$$\rho_{M \rightarrow R} = \frac{1}{N} + \frac{1}{6N}(\alpha N - \beta)s, \tag{8}$$

with  $\alpha = d + 2c - b - 2a$  and  $\beta = 2d + b + c - 4a$ . Again,  $s$  measures the strength of selection. Approximation (8) is valid if  $Ns \ll 1$  and will be called the weak selection fixation probability. The reverse probability  $\rho_{R \rightarrow M}$  that a single  $R$ -mutant reaches fixation in an otherwise homogeneous population of  $M$ -players can be derived with a symmetry argument. Our next aim is to show that there is a strong connection between these fixation probabilities and the local replicator dynamics.

**Proposition 4** (One-third law) *Let  $A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$  and  $\tilde{A}_N = A - \frac{A+A^T}{N} = \begin{pmatrix} \tilde{a} & \tilde{b} \\ \tilde{c} & \tilde{d} \end{pmatrix}$  be payoff matrices for a game with two strategies,  $R$  and  $M$ .*

1. *The weak selection fixation probabilities of the Moran process with payoff matrix  $A$  can be inferred from the replicator dynamics of the game with matrix  $\tilde{A}_N$ :*

$$\rho_{M \rightarrow R} = \frac{1}{N} + \frac{\tilde{D}}{2} \left( \tilde{x}^* - \frac{1}{3} \right) s, \quad \rho_{R \rightarrow M} = \frac{1}{N} + \frac{\tilde{D}}{2} \left( \frac{2}{3} - \tilde{x}^* \right) s. \tag{9}$$

Here,  $\tilde{x}^*$  denotes the fixed point of the replicator equation,  $\tilde{x}^* = (\tilde{c} - \tilde{a}) / (\tilde{c} - \tilde{a} - \tilde{d} + \tilde{b})$ , and  $\tilde{D}$  denotes the denominator of  $\tilde{x}^*$ . In particular, for a bistable competition ( $\tilde{a} > \tilde{c}$  and  $\tilde{d} > \tilde{b}$ ), we recover the one-third law for any group size  $N$ :

$$\begin{aligned} \rho_{M \rightarrow R} > 1/N &\Leftrightarrow \tilde{x}^* < 1/3, \\ \rho_{M \rightarrow R} > \rho_{R \rightarrow M} &\Leftrightarrow \tilde{x}^* < 1/2. \end{aligned} \tag{10}$$

2. Conversely, if the replicator equation for the game with matrix  $\tilde{A}_N$  has a fixed point  $\tilde{x}^* \in (0, 1)$ , then it can be calculated using the weak selection fixation probabilities of the Moran process for game  $A$ :

$$\tilde{x}^* = \frac{1}{3} \left( 1 + \frac{\rho_{M \rightarrow R} - 1/N}{\rho_{M \rightarrow R} + \rho_{R \rightarrow M} - 2/N} \right). \tag{11}$$

In this case, the dynamics is bistable if  $\rho_{M \rightarrow R} + \rho_{R \rightarrow M} < 2/N$  and it leads to co-existence if  $\rho_{M \rightarrow R} + \rho_{R \rightarrow M} > 2/N$ . If there is no interior fixed point, the strategy with larger fixation probability dominates the other.

*Proof*

1. The formula for  $\rho_{M \rightarrow R}$  is verified by a straight calculation: Inserting

$$\begin{aligned} \tilde{a} &= \frac{N-2}{N}a, & \tilde{b} &= \frac{N-1}{N}b - \frac{1}{N}c, \\ \tilde{c} &= \frac{N-1}{N}c - \frac{1}{N}b & \text{and} & \quad \tilde{d} = \frac{N-2}{N}d \end{aligned}$$

into the right-hand side leads to the same result as (8). The expression for  $\rho_{R \rightarrow M}$  follows from a symmetry argument, as the equilibrium frequency of  $R$  is  $1 - \tilde{x}^*$  instead of  $\tilde{x}^*$ .

2. Adding up the two equations in (9) leads to the relation

$$\frac{\tilde{D}}{2}s = 3(\rho_{M \rightarrow R} + \rho_{R \rightarrow M} - 2/N). \tag{12}$$

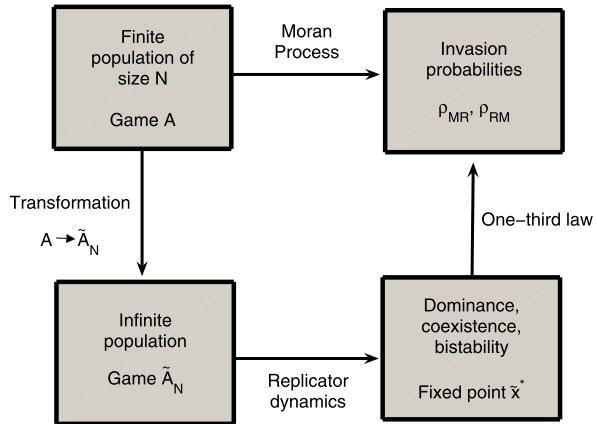
Inserting this expression into the formula for  $\rho_{M \rightarrow R}$  in (9) gives (11). Additionally, it follows that  $\tilde{D} = \tilde{c} - \tilde{a} - \tilde{d} + \tilde{b}$  has the same sign as  $\rho_{M \rightarrow R} + \rho_{R \rightarrow M} - 2/N$ . Since the fixed point  $\tilde{x}^* \in (0, 1)$  exists if and only if  $(\tilde{a} - \tilde{c})(\tilde{d} - \tilde{b}) > 0$ , the inequality  $\rho_{M \rightarrow R} + \rho_{R \rightarrow M} > 2/N$  is equivalent to  $\tilde{c} > \tilde{a}$  and  $\tilde{b} > \tilde{d}$ , i.e. to co-existence under replicator dynamics. □

Simply speaking, and under the assumption of weak selection, this means playing a game  $A$  in a finite population of size  $N$  is the same as playing the game  $\tilde{A}_N$  in an infinite population. As soon as one knows the evolutionary outcome in one regime, one can deduce the results of the other. Thus one may use replicator dynamics to study the behaviour of finite populations (by simply using the transformation  $A \mapsto \tilde{A}_N$ , see Fig. 1). Conversely, the replicator dynamics of game  $\tilde{A}_N$  can be examined by studying the finite population dynamics of game  $A$ .

As a consequence, we will see in examples that the local replicator dynamics, despite having the form of the classical replicator system, mirrors the findings in finite populations. In particular, dominated strategies can prevail.



**Fig. 1** Connection between replicator dynamics and the Moran process. To study the game  $A$  in a finite population, one may analyze the replicator dynamics of game  $\tilde{A}_N$ , which we have called the local replicator dynamics of  $A$



### 4 Examples for the Local Replicator Dynamics

#### 4.1 The Iterated Prisoner’s Dilemma

In this section, we apply our previous results to the iterated prisoner’s dilemma (Axelrod 1984). Suppose that two players may independently decide whether to transfer a benefit  $b$  at own costs  $c$  to the co-player or not (and  $b > c$ ). Assume that this game is repeated with a constant probability  $\omega$ . We distinguish three strategies: *All D* always refuses to help, whereas *All C* always cooperates. The strategy *TFT* (*Tit for Tat*) starts with cooperation and imitates the co-player’s previous move in all subsequent rounds. Thus, we get the following average payoffs per round (for a detailed derivation see Sigmund 2010):

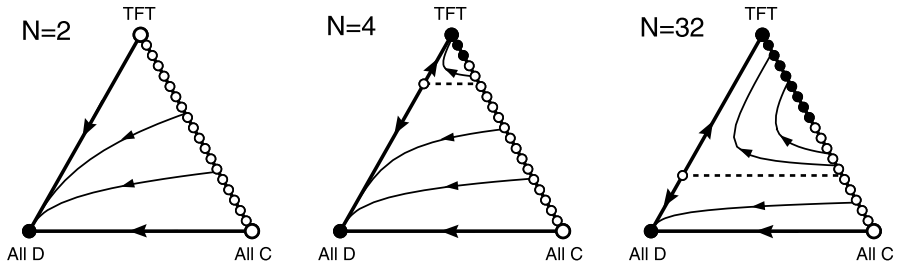
$A$	<i>All C</i>	<i>All D</i>	<i>TFT</i>
<i>All C</i>	$b - c$	$-c$	$b - c$
<i>All D</i>	$b$	$0$	$b(1 - \omega)$
<i>TFT</i>	$b - c$	$-c(1 - \omega)$	$b - c$

Obviously, the selfish strategy *All D* is always evolutionarily stable. Because  $0 < b - c$ , all players in a population of defectors would be better off if everybody cooperated. *All C* is unstable; but if the game lasts sufficiently long ( $\omega > c/b$ ), then *TFT* can resist the invasion of *All D*. However, to study the effect of playing in local groups of size  $N$ , we have to consider the modified matrix  $\tilde{A}_N$  which is up to a factor  $1/N$ :

$\tilde{A}_N$	<i>All C</i>	<i>All D</i>	<i>TFT</i>
<i>All C</i>	$(N - 2)(b - c)$	$-(N - 1)c - b$	$(N - 2)(b - c)$
<i>All D</i>	$(N - 2)b$	$0$	$(1 - \omega)[(N - 1)b + c]$
<i>TFT</i>	$(N - 2)(b - c)$	$-(1 - \omega)[(N - 1)c + b]$	$(N - 2)(b - c)$

According to the local replicator equation *TFT* is stable against invasion of defectors if and only if

$$(1 - \omega)[(N - 1)b + c] < (N - 2)(b - c).$$



**Fig. 2** The iterated prisoner’s dilemma for different group sizes. If  $N = 2$ , then any player will adopt the *All D* strategy in the long run: As both other strategies perform worse than *All D* in the direct competition, they will usually adopt the co-player’s strategy if this co-player is a defector. Increasing group size  $N$  diminishes this dilemma. As a consequence, cooperation in the iterated prisoner’s dilemma is most likely to evolve in large populations (Parameter values:  $b = 3, c = 1$  and  $\omega = 2/3$ )

Therefore, even if the game is frequently repeated ( $\omega$  close to 1), *TFT* might be unstable if its interaction neighborhood  $N$  is small (note that *TFT* is never stable for  $N = 2$ , see Fig. 2).

#### 4.2 Risk Aversion in a Coordination Game

Experiments indicate that people tend to risk-averse decisions (Kahnemann and Tversky 1979; Holt and Laury 2002; Platt and Huettel 2008): A bird in the hand is worth two in the bush. As we will see, local replicator dynamics promotes risk-aversion in coordination games. Consider the following stag hunt game (with  $r > 0$ ):

$$A = \begin{pmatrix} 1+r & 0 \\ r & 1 \end{pmatrix}.$$

Obviously this game has two pure Nash-equilibria. Owing to the higher variance of the payoffs of the first strategy, we will interpret the first strategy as risk-prone and the second as risk-averse. As the sum of each row is  $1 + r$ , rational players are exactly indifferent if they know that their co-player chooses each strategy with probability  $1/2$ . Therefore, classical replicator dynamics predicts equal basins of attraction. However, for the local replicator dynamics, we compute

$$\tilde{A}_N = \frac{1}{N} \begin{pmatrix} (N-2)(1+r) & -r \\ (N-1)r & N-2 \end{pmatrix}.$$

According to this matrix, the risk-averse strategy dominates the risk-prone strategy if  $r > N - 2$  and it has the bigger basin of attraction for  $r \leq N - 2$ . Hence, the local replicator dynamics has a clear bias toward the emergence of risk-averse strategies. The intuition behind this result is as follows: Individuals can only imitate a different strategy, if both types of players are present in the group. Therefore, a successful strategy has to perform well in mixed groups, i.e. it has to yield a notable payoff against any co-player. Overall, this effect may promote the emergence of risk-aversion, although a homogeneous population of risk-prone subjects would yield the highest possible welfare.

However, coordination to the risk-prone equilibrium is only partly observed in experiments (see, for example Straub 1995; Friedman 1996; Battalio et al. 2001) and human behaviour in coordination games seems to be very sensitive on details of the experimental setup. For example, Cooper et al. (1990) have shown that even the presence of a third, dominated strategy can alter the decisions of the subjects considerably.

### 4.3 The Dominance Paradox

Consider a cooperation game with payoffs

$$A = \left( \begin{array}{c|cc} & C & D \\ \hline C & 2+r & 1 \\ D & 1+r & 0 \end{array} \right).$$

Obviously, there is no social dilemma as the cooperative strategy dominates defective motives. Replicator dynamics thus predicts a stable population with the highest possible payoff,  $2+r$ . However, this result may be overturned for the local replicator equation:

$$\tilde{A}_N = \frac{1}{N} \begin{pmatrix} (N-2)(2+r) & N-2-r \\ N-2+(N-1)r & 0 \end{pmatrix}.$$

According to this matrix, the defective strategy dominates (!) cooperation for  $r > N-2$ . Although this result seems highly counterintuitive, it is a direct consequence of the assumed locality of interaction and replication. To see this, consider the case  $r=8$ ,  $N=4$ , for which the (original) payoff matrix becomes

$$A = \begin{pmatrix} 10 & 1 \\ 9 & 0 \end{pmatrix}.$$

If a group consists of cooperators only, everybody yields a payoff of 10; however, there is no defector in this group who could adopt this highly profitable strategy. In a group consisting of one defector and three cooperators, the average defector's payoff sums up to  $\pi_D = 9$ , compared to a cooperator's payoff of  $\pi_C = (10+10+1)/3 = 7$ . As players imitate strategies with higher payoffs, it is likely that a cooperator of this group dies and is substituted by a defector. Similarly, groups with 2 resp. 3 defectors lead to payoffs  $\pi_D = 6$  and  $\pi_C = 4$ , resp. to  $\pi_D = 3$  and  $\pi_C = 1$ . Having this in mind, the paradoxical emergence of defection becomes unsurprising.

It is important to note that this paradox is not restricted to the local replicator dynamics. Instead it is a general phenomenon for payoff-dependent imitation processes in finite populations. To see this, we calculate the weak selection fixation probabilities under the Moran process according to (8) and find (for  $N=4$ ,  $r=8$  and selection strength  $s=0.1$ ):

$$\rho_{D \rightarrow C} = 0.357 > 1/4,$$

$$\rho_{C \rightarrow D} = 0.192 < 1/4.$$

Hence, imitation processes in finite populations might induce social dilemmas where the payoff matrix itself does not reveal any problematic issue at first sight. Note that this example holds for any population size  $N$  as long as  $r > N - 2$ .

### 5 Variable Group Sizes

So far, we have assumed that all groups are of the same size. Now we focus on variable group sizes instead and consider  $N$  as a random variable. Hence, in any moment of time there may be groups of different size. The population is *well-mixed* in the sense, that any player has the same probability to become a member of a given group, i.e. the average frequency of strategy  $i$  in a group does neither depend on the group size  $N$  nor on the strategy of the co-players. Within any group, strategy updating occurs as described in the previous sections. In particular, we assume for the moment that in every group there is exactly one player who updates its strategy.

The group size  $N$  is distributed according to the probability mass function  $f(N)$ . We exclude atomic groups of one player only, i.e.  $f(1) = 0$ . Let  $\nu$  be the harmonic mean of the group sizes  $N$ , i.e.  $\nu := (\sum_{N=1}^{\infty} f(N)/N)^{-1}$ . Then we get the following generalization for random group sizes.

**Proposition 5** (Local replicator dynamics for variable group sizes) *Consider a well-mixed population of players, engaged in pairwise interactions within groups of random size  $N$ . If  $\nu < \infty$ , then the local replicator equation is given by*

$$\dot{x}_i = x_i \cdot [(\tilde{A}_\nu x)_i - x \cdot \tilde{A}_\nu x]. \tag{13}$$

*Proof* Due to Proposition 1 and our assumptions, the local replicator equation of the system is given by

$$\dot{x}_i = \sum_{N=2}^{\infty} x_i [(\tilde{A}_N x)_i - x \cdot \tilde{A}_N x] \cdot f(N),$$

which can be rewritten as

$$\begin{aligned} \dot{x}_i &= \sum_{N=2}^{\infty} x_i \left[ \left( \left( A - \frac{A + A^T}{N} \right) x \right)_i - x \cdot \left( A - \frac{A + A^T}{N} \right) x \right] \cdot f(N) \\ &= x_i [(Ax)_i - x \cdot Ax] + \sum_{N=2}^{\infty} x_i \left[ \left( -\frac{A + A^T}{N} x \right)_i + x \cdot \frac{A + A^T}{N} x \right] \cdot f(N) \\ &= x_i [(Ax)_i - x \cdot Ax] - x_i [((A + A^T)x)_i - x \cdot (A + A^T)x] \sum_{N=2}^{\infty} f(N)/N \\ &= x_i [(Ax)_i - x \cdot Ax] - x_i \left[ \left( \frac{A + A^T}{\nu} x \right)_i - x \cdot \frac{A + A^T}{\nu} x \right] \\ &= x_i \cdot [(\tilde{A}_\nu x)_i - x \cdot \tilde{A}_\nu x]. \end{aligned} \tag{□}$$

To obtain this result, we have assumed that exactly one player per group is allowed to imitate others. As a consequence, a given player in a large group is less likely to update its strategy than a player in a small group. Alternatively, we could also consider a scenario where each player is equally likely to compare its payoff with others, implying that larger groups have on average more updating events. A straightforward adaption of the proof then shows that the harmonic mean needs to be replaced by the arithmetic mean, i.e. in this case we have  $\nu = \sum_{N=1}^{\infty} Nf(N)$ .

Note that while  $N$  had to be an integer,  $\nu$  may be any positive real number with  $\nu \geq 2$ . As a consequence, we may use derivatives to study the effect of group size on the dynamics of the system. For example, by calculating  $\partial \bar{x}^*/\partial \nu$ , we may quantify the influence of  $\nu$  on equilibrium frequencies.

## 6 Discussion

Instead of the traditional assumption of a well-mixed and infinite population, we have studied a process in which individuals interact and update their strategies in randomly formed finite groups. On the one hand, such a setting can be interpreted as the mean-field approximation of a game on a lattice, where each player is connected with its  $N - 1$  neighbors only (as, for example in Nakamaru and Iwasa 2006; Rand et al. 2010). On the other hand, similar procedures are used to test human behaviour in laboratory experiments, e.g. the stranger protocol in Fehr and Gächter (2000) or the control treatment in Traulsen et al. (2010). We have shown that this process can be modelled through a replicator dynamics with a slightly modified payoff matrix.

Recent models for the evolution of cooperation in so-called *public good games* rather use a different setup. Typically, individuals are assumed to interact in randomly formed groups, but strategy updating occurs on a global level (e.g. in Brandt et al. 2006; Boyd et al. 2010), leading to classical replicator dynamics. For models of cultural learning, such a setting can be problematic: While individuals may be able to assess the performance of their everyday interaction partners, it remains unclear why they compare themselves with an abstract population average or with random role models they have never encountered before. From this perspective, local updating seems to be more intuitive. Related issues for games on graphs are discussed in Ohtsuki et al. (2007b, 2007c).

Irrespective of its derivation, we have shown that local replicator dynamics connects the Moran process with the classical replicator equation. In the frequently considered case of weak selection, any  $2 \times 2$  game  $A$  that is played in a finite population of  $N$  players can be treated *as if* it was game  $\tilde{A}_N$ , played in an infinite population. In this way, local replicator dynamics provides a comfortable tool to study games in finite populations, especially if the game under consideration allows more than two strategies. Although there has been much effort to extend the Moran process to general  $n \times n$  games (e.g. Fudenberg and Imhof 2006; Antal et al. 2009; Tarnita et al. 2009), these generalizations typically require the specification of mutation rates between strategies. Local replicator dynamics, on the other hand, is immediately defined for any number of strategies and does not involve mutation. It is important to note, however, that we have focused on games that are played pairwise. Instead, one

could also consider games where more than two players are involved. Such systems show a fascinating behaviour; at the same time they are highly complex. A first important step to explore such multi-player games is made by Gokhale and Traulsen (2010).

The modified matrix that we have studied,  $\tilde{A}_N = A - (A + A^T)/N$ , was also obtained by Lessard (2005) and Lessard and Ladret (2007), who generalized the finite population results of Nowak et al. (2004). Instead of focusing on interactions between two pure strategies,  $R$  and  $M$ , they allowed mixed strategies  $p_R$  and  $p_M$  (i.e. strategies that randomize between several pure strategies). For the Moran process, they found that selection opposes  $p_M$  replacing  $p_R$  for every  $p_M \neq p_R$  close enough to  $p_R$  if and only if  $p_R$  is evolutionarily stable for the game with payoff matrix  $\tilde{A}_N$  (with respect to the replicator dynamics). This can be regarded as another clue for the strong relationship between the game  $A$  in a finite population and the game  $\tilde{A}_N$  in an infinite population.

Interestingly, also games that are played on a graph can be represented by a modified replicator equation (Ohtsuki and Nowak 2006; Ohtsuki et al. 2007b, 2007c; Ohtsuki and Nowak 2008; Nowak et al. 2010). There it is typically assumed that players only interact with their direct neighbors. According to birth-death updating, individuals with a high payoff are likely to reproduce. The offspring replaces a randomly chosen neighbor. If each player is surrounded by  $N$  neighbors, then Ohtsuki and Nowak (2006) find that the dynamics follows a replicator equation with a modified payoff matrix  $A + B$ , where  $B$  encapsulates the impact of the population structure. The entries of  $B$  are given by the formula

$$b_{ij} := \frac{a_{ii} + a_{ij} - a_{ji} - a_{jj}}{N - 2}. \quad (14)$$

To compare this result with our findings, we multiply the modified matrix  $\tilde{A}_N$  with the constant factor  $N/(N - 2)$  (which only affects the timescale of the dynamics). With this trick, we can write the modified matrix for the local replicator dynamics as the sum of the payoff matrix  $A$  and a structure matrix  $B$  with

$$b_{ij} := \frac{a_{ij} - a_{ji}}{N - 2}. \quad (15)$$

Thus, we get the same structure matrix  $B$ , up to the diagonal terms  $a_{ii}$  and  $a_{jj}$ . As Ohtsuki and Nowak (2006) point out, these terms characterize the effect of assortativeness. In our model, we have assumed a well-mixed population and groups that are formed anew after each updating event; hence, the diagonal terms are missing in the matrix transformation for the local replicator dynamics. It remains an interesting endeavour, however, to find a general rule under which conditions games in structured population can be described with a modified replicator equation.

Since the correction term in the definition of  $\tilde{A}_N$  is of order  $1/N$ , local replicator dynamics only results in a minor correction if players interact with a large sample of the population. However, for small groups, there can be considerable differences, compared to the classical replicator dynamics. As we have seen, imitation processes in finite populations may lead to the evolution of dominated strategies. In particular,

for the game with payoff matrix

$$A = \left( \begin{array}{c|cc} & C & D \\ \hline C & 10 & 1 \\ D & 9 & 0 \end{array} \right),$$

a homogeneous population of defectors is evolutionarily stable if the population size  $N$  is small. This result may be attributed to spite: Playing  $D$  instead of  $C$  implies a small cost for oneself, but harms a cooperative co-player considerably. Overall, this may transform a win-win situation into a lose-lose situation. However, if this game is played in the laboratory, I would rather predict a cooperative equilibrium, as not only the whole population benefits from switching to cooperation but also each player individually.

This raises the question whether the local replicator equation (and equivalently, the Moran process) are good approximations on human strategy updating (for an interesting experiment on that issue see Traulsen et al. 2010). The dominance paradox, as described above, relies on the assumption that individuals blindly copy the strategy of co-players with a higher payoff, irrespective of the consequences this might have on the own future payoff. Personally, I believe that individuals have more foresight when they opt for a new strategy. Human strategy updating involves both—imitation and calculation. Hence, if evolutionary models should also account for cultural learning, then the game theoretical toolbox has to evolve further.

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## Appendix: An Alternative Derivation of the Local Replicator Equation

Local replicator dynamics can also be derived from a birth-death process, instead of imitation updating. Again, we assume that players interact within groups of size  $N$ . After those interactions, one player of each group is chosen to reproduce, proportional to its fitness. The offspring replaces a randomly chosen member of the same group.

If  $d_i(\vec{n})$  denotes the probability that a player with strategy  $i$  is chosen to die and  $b_j(\vec{n})$  is the corresponding probability that an individual with strategy  $j$  is born, then the expected change of players with strategy  $i$  within this group  $\vec{n}$  is given by

$$\Delta n_i = (1 - d_i(\vec{n})) \cdot b_i(\vec{n}) - d_i(\vec{n}) \cdot (1 - b_i(\vec{n})) = b_i(\vec{n}) - d_i(\vec{n}).$$

The birth probability of an individual depends on its fitness  $f_i(\vec{n})$ , which is a sum of baseline fitness (normalized to 1) and the payoff of this strategy,  $f_i(\vec{n}) = 1 + s\pi_i(\vec{n})$ . Hence, if  $\bar{f}(\vec{n})$  denotes the average fitness in the group, i.e.  $\bar{f}(\vec{n}) = (n_1 f_1(\vec{n}) + \dots + n_k f_k(\vec{n}))/N$ , the birth probability is given by  $b_i(\vec{n}) = \frac{n_i f_i(\vec{n})}{N \bar{f}(\vec{n})}$ . We note that  $\sum_{i=1}^k b_i(\vec{n}) = 1$ . Players die randomly, irrespective of their payoff and,

therefore, we may write the death probability as  $d_i(\vec{n}) = \frac{n_i}{N}$ . Thus, we may conclude that

$$\Delta n_i = b_i(\vec{n}) - d_i(\vec{n}) = \frac{n_i}{N} \frac{f_i(\vec{n}) - \bar{f}(\vec{n})}{\bar{f}(\vec{n})} = \frac{n_i}{N} [\pi_i(\vec{n}) - \bar{\pi}(\vec{n})] \cdot s + \mathcal{O}(s^2).$$

Again, we have to sum up these expected changes within one group over all possible groups of size  $|\vec{n}| = N$ . In the limit of weak selection, this reproduces the local replicator equation in the form of (6):

$$\dot{x}_i = \sum_{|\vec{n}|=N} \frac{N!}{n_1! \dots n_k!} x_1^{n_1} \dots x_n^{n_k} \cdot \frac{n_i}{N} [\pi_i(\vec{n}) - \bar{\pi}(\vec{n})]. \tag{16}$$

*Proposition 1:* The local replicator dynamics (16) can be rewritten as

$$\dot{x}_i = x_i \cdot [(\tilde{A}x)_i - x \cdot \tilde{A}x],$$

with  $\tilde{A}_N = A - \frac{A+A^T}{N}$ .

*Proof* First we note that the local replicator equation (16) can be written as

$$\begin{aligned} \dot{x}_i &= \sum_{\substack{|\vec{n}|=N \\ n_i \geq 1}} \frac{N!}{n_1! \dots n_k!} x_1^{n_1} \dots x_n^{n_k} \cdot \frac{n_i}{N} [\pi_i(\vec{n}) - \bar{\pi}(\vec{n})] \\ &= x_i \cdot \sum_{\substack{|\vec{n}|=N \\ n_i \geq 1}} \frac{(N-1)!}{n_1! \dots (n_i-1)! \dots n_k!} x_1^{n_1} \dots x_i^{n_i-1} \dots x_n^{n_k} [\pi_i(\vec{n}) - \bar{\pi}(\vec{n})] \\ &= x_i \cdot \sum_{|\vec{n}|=N-1} \frac{(N-1)!}{n_1! \dots n_i! \dots n_k!} x_1^{n_1} \dots x_i^{n_i} \dots x_n^{n_k} [\pi_i(\vec{n}_{+i}) - \bar{\pi}(\vec{n}_{+i})]. \end{aligned}$$

In the last line, the symbol  $\vec{n}_{+i}$  denotes a group with  $n_i + 1$  players with strategy  $i$  and  $n_j$  players with strategy  $j \neq i$ . Accordingly, the last sum is taken over all possible co-players of an  $i$ -player (i.e., over all possible groups with  $|\vec{n}| = N - 1$  players), while the first sum was taken over all possible groups with  $N$  individuals. If individuals play against everybody else in their group, but not against themselves, the corresponding average payoffs are given by:

$$\begin{aligned} \pi_i(\vec{n}_{+i}) &= \frac{1}{N-1} (a_{i1}n_1 + \dots + a_{ii}n_i + \dots + a_{ik}n_k) = \sum_{l=1}^k a_{il} \cdot \frac{n_l}{N-1}, \\ \pi_j(\vec{n}_{+i}) &= \frac{1}{N-1} (a_{j1}n_1 + \dots + a_{ji}(n_i + 1) + \dots + a_{jj}(n_j - 1) + \dots + a_{jk}n_k) \\ &= \frac{a_{ji} - a_{jj}}{N-1} + \sum_{l=1}^k a_{jl} \cdot \frac{n_l}{N-1} \quad \text{for } j \neq i, n_j > 0, \end{aligned}$$



$$\begin{aligned} \bar{\pi}(\vec{n}_{+i}) &= \frac{1}{N} (n_1\pi_1(\vec{n}_{+i}) + \dots + (n_i + 1)\pi_i(\vec{n}_{+i}) + \dots + n_k\pi_k(\vec{n}_{+i})) \\ &= \frac{\pi_i(\vec{n}_{+i})}{N} + \sum_{j=1}^k \pi_j(\vec{n}_{+i}) \frac{n_j}{N} \\ &= \sum_{l=1}^k \frac{a_{il}n_l}{N(N-1)} + \sum_{l,j=1}^k \frac{a_{jl}n_l n_j}{N(N-1)} + \sum_{j=1}^k \frac{a_{ji}n_j}{N(N-1)} - \sum_{j=1}^k \frac{a_{jj}n_j}{N(N-1)}. \end{aligned}$$

Owing to the properties of the multi-nomial distribution, we have

$$\begin{aligned} \sum_{|\vec{n}|=N-1} \frac{(N-1)!}{n_1! \dots n_k!} x_1^{n_1} \dots x_n^{n_k} \cdot n_j &= (N-1)x_j, \\ \sum_{|\vec{n}|=N-1} \frac{(N-1)!}{n_1! \dots n_k!} x_1^{n_1} \dots x_n^{n_k} \cdot n_j^2 &= (N-1)(N-2)x_j^2 + (N-1)x_j, \\ \sum_{|\vec{n}|=N-1} \frac{(N-1)!}{n_1! \dots n_k!} x_1^{n_1} \dots x_n^{n_k} \cdot n_j n_l &= (N-1)(N-2)x_j x_l \quad \text{for } j \neq l. \end{aligned}$$

Thus, we obtain, due to the linearity of the payoffs:

$$\begin{aligned} &\sum_{|\vec{n}|=N-1} \frac{(N-1)!}{n_1! \dots n_k!} x_1^{n_1} \dots x_n^{n_k} \cdot \pi_i(\vec{n}_{+i}) \\ &= \sum_{|\vec{n}|=N-1} \frac{(N-1)!}{n_1! \dots n_k!} x_1^{n_1} \dots x_n^{n_k} \cdot \left( \sum_{j=1}^k a_{ij} \cdot \frac{n_j}{N-1} \right) \\ &= \sum_{j=1}^k \frac{a_{ij}}{N-1} \left( \sum_{|\vec{n}|=N-1} \frac{(N-1)!}{n_1! \dots n_k!} x_1^{n_1} \dots x_n^{n_k} \cdot n_j \right) \\ &= \sum_{l=1}^k a_{ij} x_j = (Ax)_i. \end{aligned}$$

Analogously, we may derive

$$\begin{aligned} &\sum_{|\vec{n}|=N-1} \frac{(N-1)!}{n_1! \dots n_k!} x_1^{n_1} \dots x_n^{n_k} \cdot \bar{\pi}(\vec{n}_{+i}) \\ &= \frac{N-2}{N} \sum_{l,j=1}^k x_l a_{lj} x_j + \frac{1}{N} \sum_{j=1}^k a_{ij} x_j + \frac{1}{N} \sum_{j=1}^k a_{ji} x_j \\ &= \frac{N-2}{N} \cdot x^T Ax + \frac{1}{N} (Ax)_i + \frac{1}{N} (A^T x)_i. \end{aligned}$$

Eventually, we obtain

$$\begin{aligned}\dot{x}_i &= x_i \cdot \left[ (Ax)_i - \frac{N-2}{N} \cdot x^T Ax - \frac{1}{N} (Ax)_i - \frac{1}{N} (A^T x)_i \right] \\ &= x_i \cdot [(\tilde{A}x)_i - x^T \tilde{A}x].\end{aligned}\quad \square$$

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