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► **To cite this version:**

Matthijs van Veelen. The replicator dynamics with players and population structure. *Journal of Theoretical Biology*, 2011, 276 (1), pp.78. 10.1016/j.jtbi.2011.01.044 . hal-00682408

HAL Id: hal-00682408

<https://hal.science/hal-00682408>

Submitted on 26 Mar 2012

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Author's Accepted Manuscript

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PII: S0022-5193(11)00070-1
DOI: doi:10.1016/j.jtbi.2011.01.044
Reference: YJTBI6356

To appear in: *Journal of Theoretical Biology*

Received date: 30 August 2010
Revised date: 27 January 2011
Accepted date: 27 January 2011

Cite this article as: Matthijs van Veelen, The replicator dynamics with n players and population structure, *Journal of Theoretical Biology*, doi:10.1016/j.jtbi.2011.01.044

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The replicator dynamics with n players and population structure

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January 26, 2011

Abstract: The well-known replicator dynamics is usually applied to 2-player games and random matching. Here we allow for games with n players, and for population structures other than random matching. This more general application leads to a version of the replicator dynamics of which the standard 2-player, well-mixed version is a special case, and which allows us to explore the dynamic implications of population structure. The replicator dynamics also allows for a reformulation of the central theorem in Van Veelen (2009), which claims that inclusive fitness gives the correct prediction for games with generalized equal gains from switching (or, in other words, when fitness effects are additive). If we furthermore also assume that relatedness is constant during selection - which is a reasonable assumption in a setting with kin recognition - then inclusive fitness even becomes a parameter that determines the speed as well as the direction of selection. For games with unequal gains from switching, inclusive fitness can give the wrong prediction. With equal gains however, not only the sign, but even the value of inclusive fitness becomes meaningful.

Keywords: Hamilton's rule, inclusive fitness, group selection, replicator dynamics, generalized equal gains from switching

1 Introduction

The large majority of papers that use the replicator dynamics (Taylor and Jonker, 1978) consider games with 2 players in a well-mixed population. This 2 player, well mixed setting has been enormously successful, and one of the reasons that it has been so very popular might be that the concept of an ESS is defined in Maynard Smith & Price (1973) for a 2 player game, and that this static concept implies asymptotic stability in the replicator dynamics in a population with random matching (Hofbauer, Schuster & Sigmund, 1979). Many populations however are not well-mixed, but show some assortment, and many games are played with more than 2 players. Below we will see that the replicator dynamics, as defined by Taylor and Jonker (1978), can encompass a more general setting with n players and deviations from random matching.

There are population structures that have attracted quite some attention in the literature, such as graphs (see for instance Ohtsuki et al., 2006, and references therein) or island models (starting from Wright, 1931). The population structure in this version of the replicator dynamics is different in that it simply specifies for every frequency how the population is partitioned into groups of size n , within which this n -player game is played. The payoffs that individuals get from that interaction have an effect on reproduction in global competition, which is implied by the replicator dynamics depending only on average payoffs. One way to think of the replicator dynamics with population structure is therefore that it is a degenerate haystack model, where individuals live in the haystack for only one generation, and where the distribution over the haystacks may not be completely random. A way to subdivide the population could reflect a range of ways in which groups are formed. A specific choice for a population structure in this replicator dynamics setting is a population structure with constant relatedness, which implies that relatedness remains the same during selection. This is for instance a particularly adequate reflection of a setting with kin recognition. Population structures with relatedness that varies along a trajectory are also possible.

We will see in examples how the outcome of the dynamics depends on the population structure, allowing for instance for cooperation or defection to be selected in prisoners dilemma's, but also for bi-stability or coexistence of both cooperation and defection. The replicator dynamics are therefore quite useful in revealing the consequences of assortment. With the possibility of assortative group formation, the replicator dynamics also allow for a more appealing reformulation of the central theorem in Van Veelen (2009), which claims that generalized equal gains from switching (or, in other words, additivity of fitness effects) implies that inclusive fitness gives the correct prediction. In this new version, inclusive fitness not only determines the direction, but also the speed of selection.

2 Replicator dynamics

The replicator dynamics (Taylor and Jonker, 1978, see also Weibull, 1995, Chapter 3, or Hofbauer & Sigmund, 1998, Chapter 7) is a set of differential equations that reflects the idea that strategies that perform relatively well become more abundant in the population. The derivative of the share of strategy i is given by the equation

$$\dot{x}_i = x_i (\pi(e^i, x) - \pi(x, x)) \quad (1)$$

where e^i is the unit vector that represents pure strategy i , and where x is a point on the unit simplex that represents the current population, in which x_i is the share of strategy i in

the current population, with $i = 1, \dots, k$.¹ The replicator dynamics thereby assumes that a comparison of the payoff of pure strategy i when facing the current population - $\pi(e^i, x)$ - to the average payoff of the population - $\pi(x, x)$ - determines speed and direction of selection. There are other models with population structure for which this assumption does not hold; in local interaction models it is very well possible that the average payoff of one strategy is higher than the average payoff of the other, and decreases in frequency nonetheless (see for instance Lieberman et al., 2005, Ohtsuki & Nowak, 2006a, and Ohtsuki et al, 2006).

In the original paper by Taylor and Jonker this payoff function π is not specified - other than that it is assumed to be differentiable. However, the most common way to think of this payoff function is that it reflects pairwise interaction in a well mixed population. The assumption of random matching implies that these (expected) payoffs are computed by simply weighing the payoffs of pure strategy interactions with the frequencies;

$$\pi(e^i, x) = \sum_{j=1}^k \pi(e^i, e^j) x_j \text{ and } \pi(x, x) = \sum_{i=1}^k \pi(e^i, x) x_i,$$

where the payoffs $\pi(e^i, e^j)$ of pure strategy interactions are given by a payoff matrix. This assumption is for instance made in Hofbauer, Schuster & Sigmund (1979), Weibull (1995, Chapter 3) and at some point in Hofbauer & Sigmund (1998, Chapter 7, Section 2). However, if we want to allow for departures from random matching, then that will imply that this payoff function will have to become more general.

Here we will assume n players, 2 strategies and any kind of group formation. Having n players allows this to be a model where behaviour affects all members of a whole group. If we allow for groups of any size and for non-random group formation, then it will be helpful to restrict ourselves to only 2 strategies in order to keep notation and derivations tractable (see Hauert et al., 2006, and Pacheco et al, 2009, for the complexity that can arise with specific subsets of n -player games with 2 strategies already in the absence of population structure, and Gokhale & Traulsen, 2010, for the dynamic complexity that can arise with more than 2 players as well as more than 2 strategies, also in the absence of population structure). With only two strategies, we will give them simple and familiar names C and D , even though for some games it may not be clear what the more cooperative strategy would be.

It will be useful to characterize the population by its shares of groups of different compositions (see also Van Veelen, 2009, 2011). Groups can be composed of 0 cooperators and n defectors, 1 cooperator and $n - 1$ defectors, and so on, and a population state will be characterized by the frequencies of those different types of groups. They are denoted by $f_i, i = 0, \dots, n$, where f_i is the frequency of groups with i cooperators and $n - i$ defectors in it. In order for $f = (f_0, \dots, f_n)$ to be a consistent population state, these frequencies have to satisfy the following conditions; $0 \leq f_i \leq 1$ for all i and $\sum_{i=0}^n f_i = 1$. We say that f finds itself on the (n -dimensional) unit simplex Δ if it indeed satisfies these conditions, but it is important to stress that this simplex has a different interpretation than the familiar simplex that is used with the standard application of the replicator dynamics (see for instance Weibull, 1995). While the vertices in the standard replicator dynamics represent population states in which only one strategy is present, the vertices of this simplex represent states where all groups have the same composition; for instance $f = (0, 1, 0, \dots, 0)$ represents a population state where all groups have exactly 1 cooperator in them.

The frequency of strategy C in the overall population is denoted by p and can be computed in a straightforward way; $p = \frac{1}{n} \sum_{i=0}^n i f_i$.

¹Here I more or less follow the notation from Weibull (1995). In Taylor & Jonker's (1978) notation, Equation (1) is written as $\dot{s}_i = s_i [F(i|s) - F(s|s)]$.

A population structure will be a function \widehat{f} that maps frequencies p onto population states. This function reflects how these strategies C are distributed over different groups.

$$\widehat{f} : [0, 1] \rightarrow \Delta$$

Of course the population state on the simplex that \widehat{f} associates with a frequency p has to be consistent with that frequency; the function \widehat{f} has to satisfy $\frac{1}{n} \sum_{i=0}^n i \widehat{f}_i(p) = p$ for all $p \in [0, 1]$. The set of population structures is therefore $S = \left\{ \widehat{f} : [0, 1] \rightarrow \Delta \mid \frac{1}{n} \sum_{i=0}^n i \widehat{f}_i(p) = p \forall p \in [0, 1] \right\}$. In order to guarantee existence and uniqueness of solutions, we will assume that this function \widehat{f} is Lipschitz continuous.

With only two strategies, it is enough to define one differential equation for the frequency of one of the two strategies. If strategy 1 is to play C , we can write $\overline{\pi}_C$ for $\pi(e^1, x)$ - the (expected) payoff of playing strategy C ; $\overline{\pi}_D$ for $\pi(e^2, x)$ - the (expected) payoff of playing strategy D ; and $\overline{\pi}$ for $\pi(x, x)$ - the average payoff over the whole population. The replicator equation then becomes:

$$\begin{aligned} \dot{p} &= p(\overline{\pi}_C - \overline{\pi}) \\ &= p(\overline{\pi}_C - (p\overline{\pi}_C + (1-p)\overline{\pi}_D)) \\ &= p(1-p)(\overline{\pi}_C - \overline{\pi}_D) \end{aligned} \quad (2)$$

In order to compute $\overline{\pi}_C$ and $\overline{\pi}_D$ we need to know the payoffs of the game and the composition of the population. The game payoffs are denoted by $\pi_{C,i}$, $i = 1, \dots, n$ and $\pi_{D,i}$, $i = 0, \dots, n-1$, which are the payoffs to a cooperator, resp. defector, if there are in total i cooperators in a group. With population structure \widehat{f} , the payoff of playing strategy C now becomes $\overline{\pi}_C = \frac{1}{np} \sum_{i=1}^n i \cdot \widehat{f}_i(p) \cdot \pi_{C,i}$, and the payoff of playing strategy D becomes $\overline{\pi}_D = \frac{1}{n(1-p)} \sum_{i=0}^{n-1} (n-i) \cdot \widehat{f}_i(p) \cdot \pi_{D,i}$. If we fill those in in Equation 2 we get

$$\dot{p} = p \left(\frac{\sum_{i=1}^n i \cdot \widehat{f}_i(p) \cdot \pi_{C,i}}{np} - \left[\frac{\sum_{i=1}^n i \cdot \widehat{f}_i(p) \cdot \pi_{C,i} + \sum_{i=0}^{n-1} (n-i) \cdot \widehat{f}_i(p) \cdot \pi_{D,i}}{n} \right] \right) \quad (3)$$

This differential equation for the frequency p together with the population structure \widehat{f} defines the dynamics on the simplex. A trajectory on the simplex is a mapping $f : \mathbb{R}^+ \rightarrow \Delta$ and describes the evolution of the frequencies of the different types of groups; $f(t) = (f_0(t), \dots, f_n(t))$. This trajectory must satisfy

$$f(t) = \widehat{f}(p(t))$$

with \dot{p} satisfying Equation 3.

If we assume that \widehat{f} is Lipschitz continuous on $[0, 1]$, then one can easily show that the right hand side of (3) is also Lipschitz continuous on $[0, 1]$ (see Appendix A). Therefore, by Theorem 6.1 in Weibull (1996), the system defined by (3) has a unique solution (see also Hirsch & Smale, 1974). Note that equation (3) implies that $\dot{p} = 0$ for $p = 0$ and for $p = 1$, which is most easily seen in the last line of equation (2). Because the right hand side of (3) is Lipschitz continuous on $[0, 1]$, solutions starting in $p = 0$ or $p = 1$ remain (and have been) there forever.

3 Simple examples of population structures

3.1 Random matching

If we take $n = 2$ and functions f_i that reflect random matching, this brings us back in the standard replicator dynamics setting. The population structure \hat{f} that goes with random matching is $\hat{f}_0(p) = (1-p)^2$, $\hat{f}_1(p) = 2p(1-p)$ and $\hat{f}_2(p) = p^2$. With this \hat{f} , (expected) payoffs of C and D are

$$\begin{aligned}\bar{\pi}_C &= \frac{2 \cdot p^2 \cdot \pi_{C,2} + 1 \cdot 2p(1-p) \cdot \pi_{C,1}}{2p} = \\ &= p\pi_{C,2} + (1-p)\pi_{C,1}\end{aligned}$$

and

$$\begin{aligned}\bar{\pi}_D &= \frac{2 \cdot (1-p)^2 \cdot \pi_{D,0} + 1 \cdot 2p(1-p) \cdot \pi_{D,1}}{2(1-p)} = \\ &= p\pi_{D,1} + (1-p)\pi_{D,0}\end{aligned}$$

This is exactly what is assumed in the standard application of the replicator dynamics; the payoff of any of the two strategies is p times the payoff for meeting a C player plus $1-p$ times the payoff for meeting a D player. So this framework does indeed encompass the replicator dynamics for 2 players, 2 strategies and random matching.

3.2 Clonal interaction

Unlike the standard replicator dynamics, this framework, with general functions \hat{f} , also allows for non-random matching. We can for instance look at clonal interaction, which is a very simple extreme case. It is represented by $\hat{f}_0(p) = (1-p)$, $\hat{f}_1(p) = 0$, and $\hat{f}_2(p) = p$, which makes the following dynamics:

$$\begin{aligned}\bar{\pi}_C &= \frac{2 \cdot p \cdot \pi_{C,2}}{2p} = \\ &= \pi_{C,2}\end{aligned}$$

and

$$\begin{aligned}\bar{\pi}_D &= \frac{2 \cdot (1-p) \cdot \pi_{D,0}}{2(1-p)} = \\ &= \pi_{D,0}\end{aligned}$$

This is what we would expect with clonal interaction; every type gets the payoff of playing against itself.

3.3 Fixed relatedness and interactions with kin recognition

Yet another possibility is to take a mixture of the two extremes (random matching and clonal interaction). The parameter r determines how far away from these extremes the population structure is; $\widehat{f}_0(p) = (1 - \alpha)(1 - p)^2 + \alpha(1 - p)$, $\widehat{f}_1(p) = (1 - \alpha)2p(1 - p)$ and $\widehat{f}_2(p) = (1 - \alpha)p^2 + \alpha p$. With this particular parametrized choice of functions \widehat{f} , the average payoffs look simple again

$$\begin{aligned}\bar{\pi}_C &= \frac{2 \cdot ((1 - \alpha)p^2 + \alpha p) \cdot \pi_{C,2} + 1 \cdot (1 - \alpha)2p(1 - p) \cdot \pi_{C,1}}{2p} = \\ &= \alpha\pi_{C,2} + (1 - \alpha)\{p\pi_{C,2} + (1 - p) \cdot \pi_{C,1}\}\end{aligned}$$

and

$$\begin{aligned}\bar{\pi}_D &= \frac{2 \cdot ((1 - \alpha)(1 - p)^2 + \alpha(1 - p)) \cdot \pi_{D,0} + 1 \cdot (1 - \alpha)2p(1 - p) \cdot \pi_{D,1}}{2(1 - p)} = \\ &= \alpha\pi_{D,0} + (1 - \alpha)\{p\pi_{D,1} + (1 - p) \cdot \pi_{D,0}\}\end{aligned}$$

This compares very easily to the above cases of random matching and clonal interaction; the payoff is α times the payoff of an interaction with self plus $1 - \alpha$ the average payoff of a random interaction. It is therefore very natural to think of α as relatedness (see Appendix B). A setting with kin recognition, where interactions take place between relatives that identify each other as such, and with behaviour conditional on this recognition, fits this population structure perfectly well. With the appropriate choice for α ($\frac{1}{2}$ for siblings, $\frac{1}{8}$ for first cousins, etc.) we can assume that relatedness is indeed an exogenously given constant in the model, and therefore constant along a trajectory. Below we will therefore immediately use r instead of α .

3.4 Payoff matrix transformations

In a rather different setting, with games on regular graphs of degree $k > 2$ and different update rules, Ohtsuki & Nowak (2006b) show that the dynamics for large populations and weak selection can be described by the standard replicator dynamics with a transformed payoff matrix. In the description of their dynamics, the structure (a combination of the degree of the regular graph and an update rule) goes into the transformation of the payoff matrix; their dynamics for a game A with a certain population structure are the same as the dynamics without structure (that is, with random matching, or, in their setting, a complete graph) for a transformed game A' , where the transformation depends on the population structure.

In this paper, the population structure and the payoff matrix are kept apart. For fixed relatedness, however, one can make a similar equivalence. The dynamics for the game A with constant relatedness r are the same as for the transformed game $A' = rB + (1 - r)A$, where $b_{ij} = a_{ij}$, with fixed relatedness 0. For other population structures this will not be possible, because the r will then vary with p . Note that this transformation is not the same the transformation that we would get if we would follow Maynard Smith (1978, 1982) and replace a combination of A and relatedness r with $A'' = A + rA^T$ and relatedness 0 (see also Taylor & Nowak, 2007). Grafen (1979) pointed out that Maynard Smith's transformation was not correct and the replicator dynamics with population structure and a constant r support his equilibrium analysis of 2-player games played between relatives.

4 ESS and stability in the replicator dynamics

There are a two definitions of an ESS.

Definition 1 (Maynard Smith & Price, 1973) *A strategy x is an ESS if*

- 1) $\pi(x, x) \geq \pi(y, x) \forall y$ and
- 2) $\pi(x, x) = \pi(y, x) \Rightarrow \pi(x, y) > \pi(y, y) \forall y \neq x$,

From Maynard Smith & Price (1973) one can conclude that the payoff functions are assumed to have the form $\pi(x, y) = x^T A y$, where A is a payoff matrix, reflecting the idea of pairwise interactions and random matching. This is explicitly not the case in Taylor & Jonker (1978).

Definition 2 (Taylor & Jonker, 1978)

- A strategy x is an ESS if for every $y \neq x$ there is an $\epsilon_y \in (0, 1)$ such that $\pi(x, (1 - \epsilon) x + \epsilon y) > \pi(y, (1 - \epsilon) x + \epsilon y)$ for all $\epsilon \in (0, \epsilon_y)$*

These definitions are equivalent if we have pairwise interactions and random matching. If π is not restricted to be of the form $\pi(x, y) = x^T A y$, then one can find counterexamples that show they are no longer equivalent.²

Hofbauer, Schuster & Sigmund (1979) showed that with pairwise interactions and random matching, being an ESS (in either sense, obviously) implies asymptotic stability in the replicator dynamics. Taylor & Jonker (1978) also have a stability result, but their result uses the definition of a *regular* ESS. For this they first define the matrix A by the formula

$$a_{ij} = \frac{\partial}{\partial x_j} \pi(e^i, x)$$

The definition of a regular ESS is then:

Definition 3 (Taylor & Jonker, 1978) *A strategy x is a regular ESS if*

- 1) $\pi(e^i, x) < \pi(x, x)$ whenever $i \notin \text{supp}(x)$
- 2) $h^T A h < 0$ whenever $\text{supp}(h) \subset \text{supp}(x)$, $h \neq 0$ and $\sum_i h_i = 0$

Taylor & Jonker (1978) show that every regular ESS is an ESS in their sense, and then they show that every regular ESS is strictly stable in the replicator dynamics. Their definition of a (regular) ESS is therefore still very useful for finding stable fixed points in the replicator dynamics for n player games with population structure.

If we introduce population structure, we depart from random matching. With more general payoff functions, the two definitions of an ESS are no longer equivalent, and a population state that is a (regular) ESS in the Taylor & Jonker sense, and therefore stable in the replicator

²Take for example

$$\begin{aligned} \pi(e^1, y) &= y_2 \\ \pi(e^2, y) &= 1 - 4y_1 y_2 \end{aligned}$$

and

$$\pi(x, y) = \sum_{i=1}^2 \pi(e^i, y) x_i$$

Here $x = [\frac{3}{4}, \frac{1}{4}]$ is an ESS in Taylor & Jonker's sense; $\epsilon_y = 1 \forall y$. It is, however, not an ESS in the Maynard Smith & Price sense, since $\pi(x, y) = \pi(y, y)$ for $y = e^2$.

dynamics, may not be ESS in the Maynard Smith & Price sense.³ This implies that the definition of an ESS in the latter sense, when applied to general payoff functions, may fail to find stable fixed points of the dynamics that the former does find.

Within the set of population structures from Section 3.3, however, one can show that the two definitions are in fact equivalent. Therefore it is helpful to see that a fixed relatedness r implies that the payoff function has the form $\pi(x, y) = rx^T d + (1 - r)x^T Ay$, where d is the vector of diagonal elements of A . (This assumes that individuals play pure strategies and that a mixed population state reflects a mixture of pure strategies). With this form of the payoff function, the argument for equivalence from Weibull (1995, page 37-38) still applies. Or, in other words, Equation (1) in Taylor & Jonker (1978) holds exactly, that is, with $o(\epsilon) = 0$, not just in the case of random matching, but also with fixed relatedness. Random matching is then simply a special case of constant relatedness, with $r = 0$.

In Section 6.4 we will see that the stability result from Taylor & Jonker can indeed be quite helpful for the replicator dynamics with population structure.

5 Equal gains from switching makes inclusive fitness work

In this generalized replicator dynamics setting, we can reformulate Theorem 1 from Van Veelen (2009). The theorem restricts attention to games that satisfy generalized equal gains from switching, which is defined there as $\pi_{C,i} = 1 + ib - c$, $\pi_{D,i} = 1 + ib$, and claims that for this subset of games the direction of selection follows from Hamilton's rule. That is, strategy C is selected whenever $r\mathbf{b} - \mathbf{c} > 0$, where $\mathbf{c} = c - b$ is the net cost of the altruistic behaviour, $\mathbf{b} = (n - 1) \cdot b$ is the total benefit to all other group members, and $r = \mathbb{P}(C | C) - \mathbb{P}(C | D)$ is relatedness. The proof of that theorem can also be used for the (generalized) replicator dynamics version:

Theorem 4 *If the payoff function satisfies generalized equal gains from switching, then the direction of selection at any frequency p in any well-defined generalized replicator dynamics follows from Hamilton's rule, with $\mathbf{c} = c - b$, $\mathbf{b} = (n - 1) \cdot b$ and $r = \mathbb{P}(C | C) - \mathbb{P}(C | D)$.*

Proof. It is enough to notice that the replicator dynamics satisfy payoff monotonicity (see Van Veelen 2011 for a definition), and that the proof in Van Veelen (2009) shows that Hamilton's rule and satisfying payoff monotonicity are equivalent. Note that the frequency dependence of costs and benefits are suppressed for clarity, but bringing it back in would not change the result. ■

With a further restriction on the functions \hat{f} , we can even give a straightforward characterization of the actual trajectories. This further restriction is that \hat{f} implies a constant r . If it does, then r is constant along every trajectory, and with generalized equal gains from switching, the direction of selection is also the same along any trajectory. (Figures for the examples in Section 6 may help to form an intuition).

³The counterexample against equivalence can be used again. $A = \begin{bmatrix} 0 & 1 \\ -1 & -3 \end{bmatrix}$ for $x = [\frac{3}{4}, \frac{1}{4}]$, and with $h_2 = -h_1$ we get $h^T Ah = -3(h_1)^2$. Therefore x is a regular ESS, and with Taylor & Jonker's result, it is also stable in the replicator dynamics. However, it is still not an ESS in the Maynard Smith & Price sense.

CONSTANT r

\hat{f} implies a constant r if r is the same for all $p \in [0, 1]$

where $r = \mathbb{P}(C | C) - \mathbb{P}(C | D)$ (see Van Veelen (2009) and Appendix B. The appendix also explains why a constant r implies that r cannot be smaller than 0).

A constant r is not a mathematical necessity. Appendix C gives an example of a function \hat{f} for which r changes with p . If we however do assume a constant r , then the following theorem shows that there is a subset of games for which inclusive fitness characterizes the whole dynamics. Inclusive fitness even becomes a parameter (K) in the solution of the replicator equation that describes trajectories.

Theorem 5 *If \hat{f} implies a constant r and the game satisfies generalized equal gains from switching, then the solution of the replicator dynamics is given by*

$$\begin{aligned} p(t) &= \frac{1}{1 + \frac{1-p_0}{p_0} e^{-Kt}} \\ f(t) &= \hat{f}(p(t)) \end{aligned}$$

where $K = r \cdot \mathbf{b} - \mathbf{c}$, and $\mathbf{b} = (n-1)b$ and $\mathbf{c} = c - b$

Proof. Inspection of the proof in Van Veelen (2009) shows that

$$\bar{\pi}_C = 1 - c + b + (n-1)b\mathbb{P}(C | C)$$

and

$$\bar{\pi}_D = 1 + (n-1)b\mathbb{P}(C | D)$$

which implies that

$$\begin{aligned} \bar{\pi}_C - \bar{\pi}_D &= (n-1)[\mathbb{P}(C | C) - \mathbb{P}(C | D)]b + b - c \\ &= (n-1)rb + b - c \\ &= r \cdot \mathbf{b} - \mathbf{c} = K \end{aligned}$$

With Equation (3) we then find that

$$\begin{aligned} \dot{p} &= p(1-p)[\bar{\pi}_C - \bar{\pi}_D] \\ &= p(1-p)K \end{aligned}$$

It is easily verified that $p(t)$ as defined in the theorem indeed is the solution to this differential equation with initial frequency $p(0) = p_0$. ■

Note that the requirements in this theorem are restrictions on the population structure \hat{f} as well as on the game, and that inclusive fitness K now determines the direction as well as the speed of selection.

6 Simple examples of games with population structures

Before we go to the actual examples, that all assume a constant r and are games with 2 players, there is one observation that might be worth making. With random matching we know that adding a constant to all entries of one column in a payoff matrix is inconsequential for the properties of the replicator dynamics. With assortative matching this is no longer the case. If we solve $\bar{\pi}_C = \bar{\pi}_D$ for a 2-player game, and the solution lies in $[0, 1]$, then we have found a fixed point of the replicator dynamics. This solution is given by

$$p = \frac{r(a-d) + (1-r)(b-d)}{(1-r)(-a+b+c-d)},$$

where we replaced the payoff matrix $\begin{bmatrix} \pi_{C,2} & \pi_{C,1} \\ \pi_{D,1} & \pi_{D,0} \end{bmatrix}$ by $\begin{bmatrix} a & b \\ c & d \end{bmatrix}$ for convenience. (This is Equation (6) in Grafen, 1979). Here we see that with $r = 0$ indeed this p remains the same if we add a constant to b as well as d , or to a as well as c . However, for $r \neq 0$ this is no longer the case. With population structure, the dynamics will therefore typically be affected by adding a constant to a column of the payoff matrix.

6.1 Coordination game

For the first example we take a coordination game.

$$\begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$$

This gives us

$$\begin{aligned} \bar{\pi}_C &= r + (1-r)p \\ \bar{\pi}_D &= r + (1-r)(1-p) \end{aligned}$$

and therefore

$$\dot{p} = p(1-p)(1-r)(2p-1)$$

This implies that relatedness slows down the speed of selection here.

Not only the speed of selection can be affected by assortment in a coordination game. If we replace the payoff matrix by

$$\begin{bmatrix} 1 & 0 \\ 0 & L \end{bmatrix}$$

we get

$$\begin{aligned} \bar{\pi}_C &= r + (1-r)p \\ \bar{\pi}_D &= [r + (1-r)(1-p)]L \end{aligned}$$

which implies that $\bar{\pi}_C = \bar{\pi}_D$ for

$$p = \frac{L-r}{(1-r)(1+L)}$$

assuming that $p \in [0, 1]$. This implies that of the two basins of attraction, the size of the larger one is increased further by assortment, while the smaller one is decreased in size.

6.2 Anti-coordination game

For the second example we take an anti-coordination game.

$$\begin{bmatrix} 0 & 1 \\ L & 0 \end{bmatrix}$$

This gives us

$$\begin{aligned} \bar{\pi}_C &= (1-r)(1-p) \\ \bar{\pi}_D &= (1-r)pL \end{aligned}$$

and therefore

$$\dot{p} = p(1-p)(1-r)(1-(L+1)p)$$

This implies that for a given L , all assortment does is slow down the speed of selection. The equilibrium frequencies are determined by L , regardless of the r ;

$$p = \frac{1}{1+L}$$

6.3 Prisoners dilemmas with equal gains from switching

Theorem 2 implies that if we have a population structure \hat{f} that has constant relatedness and a game with equal gains from switching, then the direction of selection is the same at every point of the trajectory. This is illustrated on the simplex below. Note that this simplex does not reflect the same as the simplices that are used with standard replicator dynamics, where vertices are pure strategies. Here vertices are population states where all groups have the same composition; in the left down corner the population state is $f = (1, 0, 0)$, which implies that all groups have 0 cooperators in them, which in turn implies that $p = 0$. The top vertex is $f = (0, 1, 0)$, which implies that all groups have 1 cooperator in them, and $p = 0.5$. The right down vertex is $f = (0, 0, 1)$, which implies that all groups have 2 cooperators in them, and $p = 1$.

Relatedness is constant on the blue lines, as well as on the green line. It is 1 for the line at the bottom of the figure, where f_1 is always zero. This means that all groups are either all cooperator groups or all defector groups, and all individuals therefore find themselves in homogeneous groups. It is $\frac{1}{2}$ for the middle blue line, and 0 for the highest blue line, which thereby represents random matching. The green line represents $r = \frac{1}{4}$. Lines with equal frequency p are drawn in grey.

Suppose we have a game for which $\frac{c}{b} = \frac{1}{4}$, for instance the game with payoff matrix⁴

$$\begin{array}{cc} & C & D \\ C & 4 & 0 \\ D & 5 & 1 \end{array}$$

Then all trajectories with population structures with a constant $r < \frac{1}{4}$ end up in the down left corner, where $p = 0$. Those trajectories lie above the green line. All trajectories for population

⁴In the definition of generalized equal gains from switching in Van Veelen (2009), b and c are gross benefits per individual (including self) and gross costs, while \mathbf{b} and \mathbf{c} are total benefits to all others (not including self) and net costs; $\mathbf{b} = (n-1)b$ and $\mathbf{c} = c - b$. We arrive at this payoff matrix with $n = 2$, $b = 4$ and $c = 5$, which implies $\mathbf{b} = (2-1)4 = 4$ and $\mathbf{c} = 5 - 4 = 1$.

structures with $r > \frac{1}{4}$ go to the down left corner, where $p = 1$. These trajectories lie below the green line.

Figure 1. With a population structure that has a constant r and a game that has equal gains from switching, the direction of selection is the same everywhere on a line with constant r . The green line reflects Hamilton's rule for a game with $\frac{c}{b} = \frac{1}{4}$. All population structures with $r < \frac{1}{4}$ imply trajectories that end up in $p = 0$ and all population structures with $r > \frac{1}{4}$ imply trajectories that end up in $p = 1$.

6.4 Prisoners dilemmas with unequal gains from switching

If we either depart from equal gains from switching, or choose a population structure that does not imply a constant r , then the direction of selection will not necessarily always be the same at every point of the same population structure, as it is in Figure 1. In this example we will assume, as before, that r is constant along trajectories, but allow for the game not to have equal gains from switching. We therefore borrow the payoff matrix from Queller (1985).

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{array}{cc} b - c + d & -c \\ b & 0 \end{array} \end{array}$$

If $b > c > 0$ and $d < c$ this remains a prisoners dilemma. If $d \neq 0$ then it has unequal gains from switching. For the figures below we take $c = 1$, $b = 2$ and allow for d to vary.

In Van Veelen (2011) we have derived that the direction of selection is given by the following rule: $\dot{p} > 0$ if and only if $-c + br + d(r + (1 - r)p) > 0$. I refer to this rule as Queller's rule, because with the translation step in Van Veelen (2011) it coincides with the adjusted version of Hamilton's rule that Queller (1985) gives.

There are different possibilities for the dynamics. If $-c + rb + (r + (1 - r)p)d > 0$ for all $p \in [0, 1]$, then cooperation is selected. This is illustrated with the picture below.

Figure 2. The green line represents the Queller threshold for $d = \frac{1}{2}$. The blue line represents a constant r , with $r = \frac{1}{2}$. Because the blue line is below the green line everywhere, selection takes the population to the down right corner, where $p = 1$.

If $-c + rb + (r + (1 - r)p)d < 0$ for all $p \in [0, 1]$, then cooperation is selected against. This is illustrated with the picture below.

Figure 3. The green line represents the Queller threshold for $d = -\frac{1}{2}$. The blue line represents a constant r , with $r = \frac{1}{2}$. Because the blue line is above the green line everywhere, selection takes the population to the down left corner, where $p = 0$.

If there is a $p \in (0, 1)$ such that $-c + rb + (r + (1 - r)p)d = 0$, then we have bi-stability if $d > 0$. Both the down left corner ($p = 0$) and the down right corner ($p = 1$) are stable.

Figure 4. The green line represents the Queller threshold for $d = 0.8$. The blue line represents a constant r , with $r = \frac{1}{4}$. In this case there is bi-stability.

If there is a $p \in (0, 1)$ such that $-c + rb + (r + (1 - r)p)d = 0$, but now with $d < 0$, then there is a stable mixture. This is a little hard to see in the picture, but it is easy to imagine that the way the lines cross is different from Figure 5.

Figure 5. The green line represents the Queller threshold for $d = -\frac{1}{2}$. The blue line represents a constant r , with $r = \frac{5}{7}$.

Two final remarks are to be made. The first is that with Taylor & Jonker's (1978) definition of a regular ESS, we can already see that for $d < 0$ there is a range of r 's such that there is bi-stability, while coexistence is impossible, and that for $d > 0$ it is the reverse. If we combine the payoff matrix from Queller with a population structure that has a constant relatedness r , then we can easily derive that the matrix A as defined in Taylor & Jonker is $(1 - r)$ times Queller's payoff matrix. With $h_2 = -h_1$ we get $h^T A h = (1 - r)(h_1)^2 d$. That implies that condition 2) from the definition of a regular ESS is always satisfied if $d < 0$, regardless of the r , and never satisfied if $d > 0$, again regardless of the r . If a line that reflects a constant r (blue lines in the pictures) intersects with the line that represents the threshold (green lines in the pictures), then condition 1) is satisfied at the intersection. Together that implies, on the one hand, that if $d < 0$, then such an intersection is always a regular ESS, and hence stable. On the other hand, if $d > 0$ then condition 2) is never satisfied, and the intersection is unstable. This implies bi-stability of C and D because there can be only one intersection for a given r .

The second remark is that the dynamics for game A with constant relatedness r are the same as the dynamics for the transformed game $A' = rB + (1 - r)A$, where $b_{ij} = a_{ij}$, with constant relatedness 0. For this game, the transformed payoff matrix is

$$A' = r \begin{bmatrix} b - c + d & b - c + d \\ 0 & 0 \end{bmatrix} + (1 - r) \begin{bmatrix} b - c + d & -c \\ b & 0 \end{bmatrix} = \begin{bmatrix} b - c + d & -c + r(b + d) \\ (1 - r)b & 0 \end{bmatrix}$$

Filling in the parameter values for the four cases, we see that this indeed has four possibilities: C can dominate D , D can dominate C , we can have bi-stability and coexistence.

6.5 What do we learn from these simple examples?

A population structure \hat{f} assigns a population state f to every frequency p . Such a population structure therefore gives us lines on the simplex, and in the examples above, these were all blue lines. The thresholds, on the other hand, separate the simplex in population states for which cooperation is selected and population states for which cooperation is not selected. These thresholds are drawn as green lines in the examples above.

If we combine the prisoners dilemma that has equal gains from switching with a population structure that has a constant r , then these lines have the same shape. For every line that comes with a constant r we can find a cost-benefit ratio $\frac{c}{b}$ such that the threshold coincides with that line (just choose $\frac{c}{b} = r$). If this is the case, then one can separate population structure and fitness effects in the sense of Van Veelen (2011). That is, we can just look at the game characteristics, summarize those with a single number ($\frac{c}{b}$), look at the population structure, summarize that with a single number too (r) and compare those two numbers in order to determine the direction of selection (cooperation is selected if $r > \frac{c}{b}$). The example with the prisoners dilemma with *unequal* gains from switching however shows that such a clean separation of population structure and fitness effects is certainly not always possible.

A setting with kin recognition (Example 2.3) justifies a constant r . If that is combined with a game that has equal gains from switching, this gives the situation of Example 6.3, where both types of lines coincide. It seems that for most other situations it would be hard to think of reasons why the lines that represent population structure would coincide with the lines that represent selection thresholds. We expect that the dynamics therefore typically are more complicated than those of Example 6.3.

Queller (1985) uses the Price equation to derive a condition for the selection of cooperation for his payoff matrix. In Van Veelen (2005) I have raised objections to this approach, and in Van Veelen (2011) I derived a condition for the same game, but then without the Price

equation. Combined with a way to translate his condition into mine and vice versa, we find that these rules are actually the same. However, from the way Queller's rule looks, the rich dynamic possibilities are not at all visible. The generalized replicator dynamics, on the other hand, does give us a complete dynamics. The condition for the selection of cooperation that is derived *without* using the Price equation then allows us to identify whether or not the dynamics has interesting properties, such as bi-stability or stable mixed states.

It also shows that Queller's rule is not something that is generally valid, as the derivation with the Price equation seems to suggest, but that it is the result of an actual model assumption. It follows from the assumption of payoff monotonicity, which is by definition satisfied by the replicator dynamics.

7 Conclusion

The replicator dynamics is a central concept in evolutionary game theory. Here we applied the replicator dynamics to games with more than 2 players in a setting that departs from random matching. This allows us to incorporate population structure, which is central, but nonetheless not explicitly modelled in group selection models such as for instance those by Hamilton (1975), Nunney (1985) and Wilson and Dugatkin (1997). Their models do give n -player games, but are not explicit about the population structure. In these generalized replicator dynamics population structure is explicit. Although there are also many models with population structure that do not fit the replicator dynamics, it is very worthwhile to also have a version of the replicator dynamics with population structure. Amongst other things, it allows us to understand when inclusive fitness gives the correct prediction and when it does not. With generalized equal gains from switching and constant relatedness along a trajectory, inclusive fitness becomes a parameter in the solution mapping of the generalized replicator dynamics that determines the direction as well as the speed of selection. The result thereby shows that the prerequisites for inclusive fitness to give the correct prediction are rather restrictive, but if they are satisfied, then not only the sign, but even the value of inclusive fitness becomes meaningful.

8 Acknowledgements

I would like to thank James Marshall, Julian Garcia and the editor for useful comments and two anonymous reviewer for very precise, very helpful and very accurate suggestions for improvements. They really made it a better paper.

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A Lipschitz continuity

If we rewrite the right hand side of Equation (3) only a bit, then we get

$$\dot{p} = \frac{\sum_{i=1}^n i \cdot \hat{f}_i(p) \cdot \pi_{C,i}}{n} - \left[\frac{\sum_{i=1}^n i \cdot \hat{f}_i(p) \cdot \pi_{C,i} + \sum_{i=0}^{n-1} (n-i) \cdot \hat{f}_i(p) \cdot \pi_{D,i}}{n} \right] p$$

We have assumed that \hat{f} is Lipschitz on $[0, 1]$, so all \hat{f}_i , $i = 1, \dots, n$ are Lipschitz on $[0, 1]$ too. The first term of the right hand side is a sum of Lipschitz functions multiplied by constants, so that is a Lipschitz function. The same applies to the first part of the second term. Furthermore all \hat{f}_i are bounded (they remain in $[0, 1]$ for $p \in [0, 1]$), so the first part of the second term is Lipschitz and bounded on $[0, 1]$ and the second part $-p$ obviously is also Lipschitz and bounded on $[0, 1]$, and therefore their product too, and hence the whole right hand side.

B Relatedness

In Van Veelen (2009) relatedness is defined for groups of any size as $r = \mathbb{P}(C | C) - \mathbb{P}(C | D)$. This is the difference between two conditional probabilities in a hypothetical chance experiment, where the first is the probability that a random other group member is also a cooperater if you are one yourself, and the second is the probability that a random other group member is a cooperater if you are a defector yourself. Given a population structure \hat{f} and a frequency p , this can, for general group size, be written as: $r(p) = \frac{1}{np} \sum_{i=0}^n i \cdot \hat{f}_i(p) \cdot \frac{i-1}{n-1} - \frac{1}{n(1-p)} \sum_{i=0}^n (n-i) \cdot \hat{f}_i(p) \cdot \frac{i}{n-1}$. For $n = 2$ that reduces to $r(p) = \frac{\hat{f}_2(p)}{p} - \frac{\hat{f}_1(p)}{2(1-p)}$. While the definition of r by itself only implies that $-\frac{1}{n-1} \leq r \leq 1$ (see van Veelen, 2009, page 599), a population structure with constant r implies that the lower bound is a bit tighter; now $0 \leq r \leq 1$, because it is clear that $\lim_{p \downarrow 0} r(p) \geq 0$ for every population structure \hat{f} , since $\lim_{p \downarrow 0} \hat{f}_i = 0$ for $i \geq 1$.

C An \hat{f} that does not imply a constant r

As an example of a population structure \hat{f} for which r can change, we take

$$\begin{aligned} \hat{f}_0(p) &= \begin{cases} 1 - 2p & \text{if } 0 \leq p \leq \frac{1}{2} \\ 0 & \text{if } \frac{1}{2} \leq p \leq 1 \end{cases}, \\ \hat{f}_1(p) &= \begin{cases} 2p & \text{if } 0 \leq p \leq \frac{1}{2} \\ 2(1-p) & \text{if } \frac{1}{2} \leq p \leq 1 \end{cases} \quad \text{and} \\ \hat{f}_2(p) &= \begin{cases} 0 & \text{if } 0 \leq p \leq \frac{1}{2} \\ 2p - 1 & \text{if } \frac{1}{2} \leq p \leq 1 \end{cases} \end{aligned}$$

Here $r = \mathbb{P}(C | C) - \mathbb{P}(C | D)$ is not constant;

$$r = \begin{cases} -\frac{p}{1-p} & \text{if } 0 \leq p \leq \frac{1}{2} \\ -\frac{1-p}{p} & \text{if } \frac{1}{2} \leq p \leq 1 \end{cases}$$









