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Author for correspondence:
Johann Bauer
e-mail: johann.bauer@city.ac.uk

The Stabilisation of Equilibria in Evolutionary Game Dynamics through Mutation: Mutation Limits in Evolutionary Games

Johann Bauer[1], Mark Broom[1], Eduardo Alonso[2]

[1]Department of Mathematics, City, University of London
[2]Department of Computer Science, City, University of London

The multi-population replicator dynamics (RD) is a dynamic approach to coevolving populations and multi-player games, and is related to Cross' learning. In general, not every equilibrium is a Nash equilibrium (NE) of the underlying game, and convergence is not guaranteed. In particular, no interior equilibrium can be asymptotically stable in the multi-population RD, resulting, e.g., in cyclic orbits around a single interior NE. We introduce a new notion of equilibria of RD, called mutation limits, based on a naturally arising, simple form of mutation, which is invariant under the specific choice of mutation parameters. We prove the existence of mutation limits for a large class of games, and consider a particularly interesting subclass, called attracting mutation limits. Attracting mutation limits are approximated in every (mutation-)perturbed RD, hence, offering approximate dynamic solution of the underlying game, even if the original dynamic is not convergent. Thus, mutation stabilises the system in certain cases and makes attracting mutation limits near-attainable. Hence, attracting mutation limits are relevant as a dynamic solution concept of games. We observe that they have some similarity to Q-learning in multi-agent reinforcement learning. Attracting mutation limits do not exist in all games, however, raising the question of their characterization.

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1. Introduction

Evolutionary game theory has contributed significantly to our understanding of a wide range of biological, e.g., [1,2], and social phenomena, as shown by the vast research into the evolution of cooperation and eusociality, e.g., [3], or the problem of collective action, e.g., [4]. The evolutionary game theoretic approach, formulated in [1], initially assumed a single population with intrapopulation interaction and competition for reproduction, resulting in the concept of the evolutionarily stable strategy (ESS), a refinement of the Nash equilibrium concept, where a strategy is said to be evolutionarily stable if it outperforms any other newcomer strategy in a population consisting almost entirely of players playing the former.

While the intuition underlying the notion of an ESS is dynamic, its main definition is usually given in static terms. In an effort to capture the dynamic intuition of the ESS concept, the continuous time replicator dynamics (RD), provided by [5], relates the ESS to certain stationary points, [6], albeit lacking a complete characterization. In its usual formulation, it captures the single population setting with pairwise intrapopulation interactions. However, just as the concept of an ESS has been extended to the multi-population, or multi-species, setting, e.g., [7], so has RD been formulated and analysed in the multi-population setting with intrapopulation competition (for reproduction) but *inter*population interactions (determining reproductive advantage), e.g., [8]. Forms of multi-population RD have been employed in the analysis of coevolutionary systems, such as mutualism [9], antagonistic coevolution of host-parasite systems [10,11], of institutional ecosystems [12], of the evolution of a population's sex ratio [13], or the coevolution of social behaviour and recognition [14]. It has further been linked to Cross' learning, a simple type of reinforcement learning [15].

In the context of potentially very large systems, e.g., complex ecosystems or multi-agent systems, multi-population RD is of special interest because a population's composition evolves exclusively depending on the payoffs from interactions, but independent of any information about the other populations' payoffs, their compositions, or indeed their very existence. The latter specifics affect a population's composition only through their effect on its payoffs. Borrowing the term from [16], we call this property of RD its *uncoupledness*.

In spite of RD leading to payoff-improving or even equilibrium states in certain cases, there are intuitively simple games, for which neither an ESS exists nor RD reaches any Nash equilibrium, exhibiting periodic limit or general non-convergent behaviour instead: In the usual rock-paper-scissors (RPS) game, RD has exclusively periodic orbits in the single population case and the only Nash equilibrium, an interior point, is not approached from any initial state, e.g., [2], and a range of (un)-stable situations can result [17]. Further, the two population setting results in periodic orbits, as well, and therefore does not reach the interior Nash equilibrium either. An analogue result holds for the matching pennies game, e.g., [8]. Indeed, it has been shown in [16] that no uncoupled dynamics, in particular RD, can be converging to a Nash equilibrium for all possible games. For our understanding of actual biological populations, this periodicity is not necessarily problematic. On the contrary, periodic population dynamics similar to the single-population RPS case have been observed in nature, e.g., in the common side-blotched lizard (*Uta stansburiana*) [18]. For our understanding of the conditions of behavioural convergence in multi-agent systems and their ability to solve large-scale problems such periodic behaviour is less desirable.

Although RD is intended to capture the idea of evolutionary selection, and thus is inspired by evolution, it treats mutation, an arguably central process of evolution and one of the main generators of the diversity on which selection operates, as an extremely rare event, to the degree that it is actually absent from the formulation of the dynamics, especially in the case of multiple populations, e.g., [8]. Approaches which include mutation mainly focus on the single population case [19–26], consider a payoff-adjusted RD, or a discrete time process [27], or a single discrete population [28,29], while we are not aware of an analysis of continuous-time multi-population RD with mutation, apart from [30] where certain approximations to multi-population RD are considered, with a different focus however and not linked to mutation.

We demonstrate that accounting for mutation in multi-population RD can fundamentally change the properties of the dynamics, i.e., preclude any periodicity in certain cases and, furthermore, guarantee convergence to states close to Nash equilibria, which would not be reachable under standard RD. Note that the non-existence result in [16] does not directly apply to such mutation dynamics, as it only considers Nash-convergence.

Our main interest, therefore, lies with the derivation of an uncoupled dynamics, which, on the one hand, explicitly considers mutation and, on the other hand, is as close as possible to standard RD, and with the analysis of how this mutation mechanism affects the position and stability of equilibria compared to the standard (multi-population) RD. The resulting mutation mechanism with spontaneous mutations from one type to another is of course not appropriate for all biological mutation processes. In a biological population, such spontaneous mutation between a finite number of types occurs, e.g., for single nucleotide polymorphisms, where alleles differ by only one nucleotide, with the number of possible single nucleotide polymorphisms at that position restricted to four. Furthermore, such point mutations are known to occur with a non-negligible probability [31,32] and can be significant factors in diseases, [32,33], e.g., sickle cell anaemia, [34,35], which also interacts with malaria parasites, [36], cystic fibrosis, [37], or β thalassemia, [38,39], and further in human cancer cells, [40,41]. There is further evidence that in *Drosophila* most such nonsynonymous point mutations are deleterious, while the rest are slightly deleterious, near-neutral, or weakly beneficial, [42], suggesting that a weak selection assumption as we employ can be reasonable for persisting polymorphisms. Considered as a learning dynamics, modifications of multi-population RD have been shown to be linked to so-called Q-learning, a more sophisticated reinforcement learning algorithm, [43]. In particular, the resulting modification can be interpreted as a mutation-like term.

The inclusion of mutation should not only further our understanding of coevolutionary multi-population systems, such as ecosystems. Its ability in certain cases to stabilise equilibria for any non-zero mutation rate, and thereby make them approachable under an uncoupled dynamics, should also be useful in the study of game theoretical solution concepts, such as ε-Nash equilibria, [44], and the formulation of conditions for the convergence of learning in multi-agent systems.

We proceed by introducing the standard multi-population RD, i.e., without mutation, and recounting some stability properties of its equilibria and their relation to game theoretic concepts, such as Nash equilibria and evolutionary stability.

We then introduce mutation and give a heuristic derivation of the specific form of mutation we consider, defining a replicator-mutator dynamics (RMD), the equilibria of which we call *mutation equilibria*. For fixed mutation parameters, we prove the existence of equilibria of RMD, their ε-Nash property, and their uniqueness and asymptotic stability under very high mutation.

We proceed by defining the concept of limits of mutation equilibria for vanishing mutation, which we call *mutation limits*. Mutation limits and their properties are independent of any choice of specific mutation parameters. We prove the existence of mutation limits for all systems with continuously differentiable fitness functions and give a sufficient condition for a Nash equilibrium to be a mutation limit.

In order to address the question of reachability of mutation limits, we define the notion of an *attracting* mutation limit based on the asymptotic stability of the mutation equilibria by which it is approximated. Such attracting mutation limits are reachable in the sense that for any choice of mutation parameters there is an asymptotically stable mutation equilibrium arbitrarily close to the mutation limit.

We further provide a sufficient condition for a Nash equilibrium to be an attracting mutation limit. In particular, all evolutionarily stable states are attracting mutation limits, but not all attracting mutation limits are evolutionarily stable, showing the notion to be a strictly weaker property than evolutionary stability. We conclude by giving a necessary condition for attracting mutation limits, ruling out hyperbolic interior equilibria.

2. Multi-population Replicator Dynamics

In the following we consider the situation where we have a finite set of populations $I = \{1, 2, \ldots, N\}$ and each population i consists of a finite number of types which we enumerate and denote by $S_i = \{1, 2, \ldots, n_i\}$. Note that types are population-specific and numbers do not identify types across populations. The composition of a population i is then given as a vector x_i such that $x_{ih} \geqslant 0$ gives the frequency of a type $h \in S_i$ in population i. Thus, the set of possible compositions of population i is given as:

$$\Delta_i = \left\{ x_i \in \mathbb{R}^{n_i}_{\geqslant 0} \,\middle|\, \sum_{h \leqslant n_i} x_{ih} = 1 \right\}$$

For convenience, we denote the Cartesian product of the Δ_i $(i = 1 \ldots N)$ by Δ, i.e., $\Delta = \times_{i \leqslant N} \Delta_i$, and denote by Δ° the interior of Δ, i.e., $\forall i \leqslant N, h \leqslant n_i : x_{ih} > 0$. Furthermore, we set $S = \{(i,h) | i \in I \text{ and } h \in S_i\}$, such that $\Delta \subset \mathbb{R}^S$, where $\mathbb{R}^S$ denotes the set of tuples of reals indexed by S. The state of the multi-population model then is a description of the frequencies of the different types in the populations, i.e., it is given by some $x \in \Delta$.

We assume that for each population $i \in I$ and each type in that population $h \in S_i$ we have a function $f_{ih} \in \mathcal{C}^1(U, \mathbb{R})$, for $U \supset \Delta$ open, describing the reproductive rate or fitness $f_{ih}(x)$ of that type in a given state $x \in \Delta$ and we define population i's average fitness as $\bar{f}_i(x) = \sum_{h \leqslant n_i} x_{ih} f_{ih}(x)$. It should be noted that fitness is frequency-dependent in replicator dynamics models and not affected by population sizes. We further assume that there is no intraspecific interaction affecting fitness in a type-specific manner, i.e., the fitness values of types in population i are independent of the composition of population i or $\frac{\partial}{\partial x_{ik}} f_{ih}(x) = 0$ $(i \in I, h, k \in S_i)$ in keeping with the classic normal-form game settings.[1] The standard multi-population replicator dynamics, based on [45] and developed later, e.g., [8], is given by the following system of differential equations:

$$\dot{x}_{ih} = \phi_{ih}(x) := x_{ih} \left(f_{ih}(x) - \bar{f}_i(x) \right) \quad (i \in I, h \in S_i) \tag{RD}$$

We denote by $\Phi : \mathbb{R} \times \Delta \to \Delta$ the flow of (RD), i.e., for $x \in \Delta$, $\Phi(\cdot, x) : \mathbb{R} \to \Delta, t \mapsto \Phi(t, x)$ is a solution of (RD) with $\Phi(0, x) = x$. Due to our continuity assumption on f, the existence and uniqueness of Φ is clear, e.g., [46, Thm 6.1].

(a) Stationary points of the replicator dynamics

We give a short recount of some well-known properties of (RD) with regards to game theory, beginning with the main concept of game theory:

Definition 2.1 (Nash equilibrium). We call a state $x^* \in \Delta$ a *Nash equilibrium* if

$$\forall i \in I, z_i \in \Delta_i \backslash \{x_i^*\} : \bar{f}_i(x^*) \geqslant \bar{f}_i(x^*_{-i}, z_i),$$

where (x^*_{-i}, z_i) denotes the state such that

$$[x^*_{-i}, z_i]_{jk} = \begin{cases} z_{ik} & \text{if } j = i, \\ x^*_{jk} & \text{otherwise} \end{cases} .$$

We call $x^* \in \Delta$ a *strict Nash equilibrium* if all inequalities in the Nash equilibrium condition are strict.

Remark. It is clear that $x^* \in \Delta$ is a Nash equilibrium if and only if

$$\forall i \in I, h \leqslant n_i : \; g_{ih}(x^*) := f_{ih}(x^*) - \bar{f}_i(x^*) \leqslant 0.$$

Note that $g_{ih}(x)$ is exactly the coefficient of x_{ih} in (RD). Therefore, we can denote the set of Nash equilibria by $\mathcal{E} = \{x \in \Delta \,|\, g(x) \leqslant 0\}$, where the inequality is component-wise. A strict Nash

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[1] Note that this assumption is not essential for all results.

equilibrium $x^* \in \Delta$ in particular is a state where each population consists of exactly one type, i.e., for each population $i \in I$ there is exactly one type h_i such that $x^*_{ih_i} = 1$.

The following results on Nash equilibria and stationary points of (RD) are straight-forward and well-known, e.g., [8, p. 173]:

Proposition 2.2. *If* $x \in \Delta$ *is a Nash equilibrium, then* x *is a stationary point of* (RD), *i.e.,* $\phi(x) = 0$.

Proposition 2.3. *If* $x \in \Delta^\circ$ *is a stationary point of* (RD), *then* x *is a Nash equilibrium.*

(i) Stability properties of equilibria

Our special interest lies with the attainability of Nash equilibria. Therefore, we restate a few stability properties of Nash equilibria and stationary points of (RD) respectively.

Definition 2.4. We call a stationary point $x \in \Delta$ *stable*, if for every neighbourhood U of x there is a neighbourhood $V \subset U$ such that $\Phi(\mathbb{R}_{\geqslant 0}, V) \subset U$. We further call a stationary point $x \in \Delta$ *asymptotically stable* if x is stable and there is a neighbourhood V of x such that for all $y \in V$ we have $\Phi(t, y) \to x$ for $t \to \infty$.

For stable stationary points we have the following:

Proposition 2.5. *If* $x \in \Delta$ *is a stable stationary point of* (RD), *then* x *is a Nash equilibrium.*

A proof of this statement can be found in [8, Thm 5.2]. Note that this further characterization is interesting if $x \in \partial\Delta$, as stationary points on the boundary of Δ are not necessarily Nash equilibria. Furthermore, it implies that stationary points that are not Nash equilibria must be unstable and thus are harder to attain under (RD). However, note that Nash equilibria do not have to be stable. We have the following stronger characterization of asymptotically stable stationary points (with a proof in, e.g., [8, Prop. 5.13]):

Proposition 2.6. *A stationary point* $x \in \Delta$ *is asymptotically stable under* (RD) *if and only if* x *is a strict Nash equilibrium.*

For completeness, we would like to mention the relationship between stationary points of (RD) and evolutionarily stable states, where we define evolutionary stability as in [8, p. 166], equivalently to [7], as follows:

Definition 2.7 (Evolutionary Stability)**.** We call a state $x^* \in \Delta$ *evolutionarily stable* if for all $y \in \Delta$ $(y \neq x^*)$ there is some $\bar{\varepsilon}_y > 0$ such that for all $\varepsilon \in (0, \bar{\varepsilon}_y)$ and $w = \varepsilon y + (1 - \varepsilon)x^*$ we have some $i \in I$ with $\bar{f}_i(x_i, w_{-i}) > \bar{f}_i(y_i, w_{-i})$.

It is well known that in the multi-population case the concept of evolutionary stability is equivalent to that of a strict Nash equilibrium, e.g., [8, Prop. 5.1]:

Proposition 2.8. $x \in \Delta$ *is evolutionarily stable if and only if* x *is a strict Nash equilibrium.*

Therefore, we have that strict Nash equilibria are exactly the evolutionarily stable states and exactly the asymptotically stable stationary points of (RD). The dynamics (RD) will therefore not have any asymptotically stable points if the underlying game does not have any strict Nash equilibria. Furthermore, no mixed Nash equilibrium can be asymptotically stable, such that there is no guarantee that any Nash equilibrium will be approached under (RD) if the game has only mixed Nash equilibria.

3. Introducing mutation

We consider the effect of mutation for two reasons. First, the idea of evolution is intricately linked with mutation and mutation does not seem to be an extraordinary event but is to be expected. Second, a central idea in the proof that the dynamics (RD) has no interior asymptotically stable states relies on the fact that (RD) is divergence free (after suitable modification) and therefore volume preserving, [6]. However, some games, such as the matching pennies game and the standard rock-paper-scissors game, have only interior equilibria, while describing biologically relevant interspecies interactions such as host-parasite systems. The kind of mutation we consider results quite clearly in a dynamics with negative divergence. Of course, this does not guarantee asymptotically stable interior equilibria, but it opens up the possibility of such equilibria.

We will first give a motivational heuristic derivation of our specific replicator-mutator dynamics from a more general form. Afterwards, we will consider the properties of our specific dynamics and of its equilibria.

(a) Replicator-Mutator Dynamics

General mutation

In the standard replicator dynamics (RD), we assume that the offspring of individuals of some type inherit that same type. In contrast, we consider mutation as a process by which the offspring of a certain individual changes into another type (of the same population) with some probability. More precisely, we assume that the offspring of an h-type in population i mutates to a k-type in the same population with some probability $\mu_{ikh} > 0$, with $\sum_{k \leqslant n_i} \mu_{ikh} = 1$ for all populations i, and therefore:

$$\mu_{ihh} = 1 - \sum_{k \neq h} \mu_{ikh}$$

In order to represent overall mutation more clearly, we introduce *relative mutation probabilities* c_{ikh} and an overall mutation rate μ_i such that $\mu_{ikh} = \mu_i c_{ikh}$ $(h \neq k)$ and thus:

$$\mu_{ihh} = 1 - \mu_i \sum_{k \neq h} c_{ikh}$$

Here, μ_i controls the overall strength of mutation, such that for $\mu_i = 0$ there is no mutation at all, without affecting relative probabilities. We derive our specific dynamics from the general multi-population replicator-mutator dynamics as given in, e.g., [23],

$$\dot{x}_{ih} = \sum_{k \leqslant n_i} \mu_{ihk} x_{ik} f_{ik}(x) - x_{ih} \bar{f}_i(x) \tag{3.1}$$

yielding after substitution:

$$\dot{x}_{ih} = x_{ih}(f_{ih}(x) - \bar{f}_i(x)) + \mu_i \sum_{k \leqslant n_i} (c_{ihk} x_{ik} f_{ik}(x) - c_{ikh} x_{ih} f_{ih}(x)) \tag{3.2}$$

This formulation emphasizes the similarity to the standard replicator dynamics (RD) and how μ_i determines the extent to which (3.1) deviates from (RD).

Weak selection-weak mutation limit

Recall that (RD) is invariant under the addition of a background fitness for all types of a population, a property which (3.1) does not have. We therefore derive a version which is invariant under the addition of a constant background fitness. For convenience, let ${s_i}^{-1}$ denote some background fitness, where s_i can be seen as representing the selection pressure on that particular trait. Formulating (3.1) with a modified fitness function $\tilde{f}_{ih} : x \mapsto f_{ih}(x) + {s_i}^{-1}$ and suitable substitution yields a dynamics with explicit background fitness:

$$\dot{x}_{ih} = \phi_{ih}(x) + \frac{\mu_i}{s_i} \sum_{k \leqslant n_i} \left(s_i \left(c_{ihk} x_{ik} f_{ik}(x) - c_{ikh} x_{ih} f_{ih}(x)\right) + c_{ihk} x_{ik} - c_{ikh} x_{ih}\right)$$

Analogous to [6], we consider a weak selection-weak mutation limit, where the background fitness tends to infinity, i.e., the selection pressure goes to zero $s_i \to 0$, and mutation occurs on the same order as selection, i.e., $\mu_i \to 0$, such that overall:

$$\frac{\mu_i}{s_i} \to M_i > 0$$

This yields the following weak selection-weak mutation limit of (3.1), which is invariant under addition of background fitness,

$$\dot{x}_{ih} = x_{ih}(f_{ih}(x) - \bar{f}_i(x)) + M_i \sum_{k \leqslant n_i} (c_{ihk} x_{ik} - c_{ikh} x_{ih}) \tag{3.3}$$

where we refer to M_i as the *mutation rate* in population i. Note that (3.3) can also be derived from a discrete selection-mutation equation, [6]. Additionally, we assume that mutation is memoryless, i.e., $c_{ihk} = c_{ihl}$ $(k, l \neq h)$, akin to Kingman's house-of-cards model [19], so we can write c_{ih} instead of c_{ihk} and that the mutation rate is the same for every population, replacing M_i with M, resulting in the following: [2]

Replicator-Mutator Dynamics

For some fixed $c \in \Delta^\circ$ and $M \geqslant 0$, the replicator-mutator dynamics (RMD) is given by:

$$\dot{x}_{ih} = \phi^M_{ih}(x) := x_{ih}(f_{ih}(x) - \bar{f}_i(x)) + M(c_{ih} - x_{ih}) \tag{RMD}$$

It is clear that we obtain (RD) for $M = 0$. We denote by $\Phi^M : \mathbb{R} \times \Delta \to \Delta$ the flow of (RMD), i.e., for $x \in \Delta$, $\Phi^M(\cdot, x) : \mathbb{R} \to \Delta, t \mapsto \Phi^M(t, x)$ is a solution of (RMD) with $\Phi^M(0, x) = x$.

Remark. Note that Φ^M also depends on our choice of c. Throughout this section, we will consider some arbitrary but *fixed* $c \in \Delta^\circ$ and the defined concepts will depend on that choice. However, we will proceed to properties of (RMD) which are invariant under the choice of c later on.

Definition 3.1. We call $x \in \Delta$ with $\phi^M(x) = (\phi^M_{ih}(x))_{(i,h) \in S} = 0$ a *mutation equilibrium* for M. For shortness, we call x^M a mutation equilibrium if it is a mutation equilibrium for M.

Definition 3.2. We call a sequence $(x_n)_{n \in \mathbb{N}} \subset \Delta$ a sequence of mutation equilibria if there is a sequence $(M_n)_{n \in \mathbb{N}} \subset \mathbb{R}_{>0}$ with

i) $M_n \to 0$ for $n \to \infty$
ii) and x_n is a mutation equilibrium for M_n, i.e., $\phi^{M_n}(x_n) = 0$, for all $n \in \mathbb{N}$.

For ease of notation, we write such a sequence as $(x^M)_{M>0}$.

Under suitable assumptions, such sequences represent the change of a coevolutionary system under decreasing mutation rates, and we will be especially interested in the limits of such sequences of mutation equilibria and in their properties.

(b) Existence of stationary points with mutation

Lemma 3.3. *For all $M > 0$ and $c \in \Delta^\circ$ there is $x \in \Delta^\circ$, such that x is a stationary point of the replicator-mutator dynamics (RMD), i.e., $\phi^M(x) = 0$.*

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[2] Note that we can choose M_i such that $\sum_{h \leqslant n_i} c_{ih} = 1$ holds. Although we consider M as independent of the population, population-dependent mutation parameters M_i are mostly compatible with the present arguments, but would render proofs overly technical.

Proof. Note that the vector field ϕ^M points towards the interior of Δ for all $x \in \partial\Delta$. We thus have that for all $x \in \partial\Delta$ and all $t > 0$, $\Phi^M(t, x) \in \Delta^\circ$, and thus Δ is forward-invariant under the flow Φ^M, in particular, $\Phi^M(\mathbb{R}_{>0}, \Delta) \subset \Delta^\circ$. Furthermore, it is clear that Δ is nonempty, convex and compact. Using Brouwer's fixed point theorem, we can now use that if a nonempty, convex compact set is forward-invariant under a flow, then it contains a fixed point, e.g., [46, Lemma 6.8]. With $\Phi^M(\mathbb{R}_{>0}, \Delta) \subset \Delta^\circ$, we have that the fixed point has to be in Δ°. □

The following definition, e.g., as given by [44], will be useful in our later investigation:

Definition 3.4 (ε-Equilibrium). For some $\varepsilon > 0$, we call a state $x^\varepsilon \in \Delta$ an *ε-equilibrium* if

$$\forall i \in I, h \leqslant n_i : \; f_{ih}(x^\varepsilon) - \bar{f}_i(x^\varepsilon) \leqslant \varepsilon\,.$$

In relation to ε-equilibria we state the following property:

Lemma 3.5. *Let x^M be a mutation equilibrium, then x^M is an ε-equilibrium of the underlying game for $\varepsilon = M$, and in particular $\forall i \in I, h \leqslant n_i : \; f_{ih}(x^M) - \bar{f}_i(x^M) < M$.*

Proof. For $(i, h) \in S$, we have that

$$0 = \phi^M_{ih}(x^M) = x^M_{ih}(f_{ih}(x^M) - \bar{f}_i(x^M)) + M(c_{ih} - x^M_{ih}) > x^M_{ih}(f_{ih}(x^M) - \bar{f}_i(x^M)) - M x^M_{ih}$$

and thus, with $x^M \in \Delta^\circ$, we have $f_{ih}(x^M) - \bar{f}_i(x^M) < M$. □

Together with the continuity of f, we have the following:

Corollary 3.6. *Let $(x^M)_{M>0}$ be a sequence of mutation equilibria and x^* an accumulation point for $M \to 0$. Then x^* is a Nash equilibrium.*

(c) Mutation equilibria for high mutation rates

We consider some specific properties under high mutation rates which illustrate the effect of mutation on the number and stability of equilibria through its effect on the Jacobian of the replicator dynamics. Note that all equilibria of (RMD), irrespective of the specific choice of $M > 0$, lie in the interior of Δ and that ϕ^M points inward on $\partial\Delta$. We can therefore consider (RMD) as a dynamics on Δ°. We can further, for all populations i, replace x_{in_i} with $(1 - \sum_{k<n_i} x_{ik})$, and thus proceed to the resulting reduced system $\tilde{\phi}^M$ (with an analogous procedure to obtain $\tilde{\phi}$ from ϕ), which is then defined on the Cartesian product of the $(n_i - 1)$-simplices. For ease of notation, we will still use Δ to denote this reduced space. Thus, questions regarding the stability of a mutation equilibrium $x^M \in \Delta^\circ$ can be treated by considering the eigenvalues of the Jacobian $D\tilde{\phi}^M$. In particular, due to the Hartman-Grobman theorem, e.g., [46,47], we have the following useful characterization:

Remark 3.7. Let x^M be a *hyperbolic* equilibrium of (RMD), and of the reduced system $\tilde{\phi}^M$ equivalently, i.e., all eigenvalues of $D\tilde{\phi}^M(x^M)$ have non-zero real part. Then x^M is asymptotically stable if and only if all eigenvalues of $D\tilde{\phi}^M(x^M)$ have negative real part, e.g., [46, Thm 6.10]. In particular, all eigenvalues of $D\tilde{\phi}^M(x^M)$ have negative real part, if and only if all eigenvalues of $D\tilde{\phi}(x^M)$ have real part smaller than M, due to $D\tilde{\phi}^M = D\tilde{\phi} - M \cdot I$, where I is the identity matrix.

With this observation, we obtain the following:

Lemma 3.8. *There is $\underline{M} \geqslant 0$ such that for all $M > \underline{M}$ the stationary points of the replicator-mutator dynamics (RMD) are asymptotically stable. In particular, $D\tilde{\phi}^M$ is invertible everywhere on Δ.*

Proof. Note that all eigenvalues of $D\tilde{\phi}$ are bounded on Δ, in particular the real parts of the eigenvalues are bounded, as well. Then let $\underline{M}$ be an upper bound on all real parts of the eigenvalues of $D\tilde{\phi}$ on Δ°, i.e.:

$$\underline{M} = \sup\{\Re(\lambda) \mid \lambda \in \sigma(D\tilde{\phi}(x)), x \in \Delta\}$$

Let $x^M \in \Delta^\circ$ be a mutation equilibrium for some $M > \underline{M}$. As noted, the Jacobian of $\tilde{\phi}^M$ satisfies $D\tilde{\phi}^M(x) = D\tilde{\phi}(x) - M \cdot I$ for all $x \in \Delta$. In particular, for all eigenvalues $\lambda^M \in \sigma(D\tilde{\phi}^M(x^M))$ we have that $\lambda^M + M \in \sigma(D\tilde{\phi}(x^M))$ and hence $\Re(\lambda^M) + M \leqslant \underline{M}$, and thus $\Re(\lambda^M) < 0$. Therefore, all eigenvalues of $D\tilde{\phi}^M(x^M)$ have strictly negative real parts and with remark 3.7, x^M is asymptotically stable. ☐

Remark. Note that that the $\underline{M}$ in the previous lemma 3.8 is independent of the choice of $c \in \Delta^\circ$, thus giving a lower bound on the mutation rate above which all equilibria are asymptotically stable independent of $c \in \Delta^\circ$.

Uniqueness of mutation equilibria for high mutation rates

For very high mutation ($M > \underline{M}$) we further obtain that mutation equilibria are unique and that there is a continuously differentiable function mapping mutation rates to mutation equilibria. We first consider the following lemma (proven in the appendix as corollary A.4):

Lemma 3.9. *Let $c \in \Delta^\circ$ and $\underline{M}$ from lemma 3.8. Let x^M be a mutation equilibrium for some $M > \underline{M}$. Then there is a unique function $\mathcal{M} : (\underline{M}, \infty) \to \Delta$ such that $\mathcal{M}(M) = x^M$ and for all $m \in (\underline{M}, \infty)$, $\mathcal{M}(m)$ is a mutation equilibrium for m. In particular, $\mathcal{M}$ is continuously differentiable and $\mathcal{M}(m) \overset{m\to\infty}{\longrightarrow} c$.*

Note that this does not guarantee any uniqueness of equilibria, yet, only the uniqueness of functions passing through a given equilibrium. The uniqueness of mutation equilibria for high mutation rates is then obtained in the next step from the fact that we have uniqueness at least for some mutation rate (proven in the appendix as proposition A.5):

Proposition 3.10. *Let $c \in \Delta^\circ$ and $\underline{M}$ from lemma 3.8. For all $M > \underline{M}$, the replicator-mutator dynamics (RMD) has a unique mutation equilibrium. The unique map $\mathcal{M} : M \mapsto x^M$ is continuously differentiable on $(\underline{M}, \infty)$.*

Remark 3.11. Note that the main achievement of proposition 3.10 is to extend the uniqueness of equilibria beyond any Lipschitz constant of $\tilde{\phi}$ to $(\underline{M}, \infty)$, i.e., to the interval where $D\tilde{\phi}^M$ is guaranteed to be invertible. Furthermore, if $D\tilde{\phi}^M(x^M)$ is invertible for all $M \in (a, \infty)$ and corresponding mutation equilibria x^M then the uniqueness extends to (a, ∞). In fact, if $a = 0$ then there is a unique sequence of mutation equilibria $(x^M)_{M>0}$ for $c \in \Delta^\circ$ since it is induced by the function $\mathcal{M}$.

For a fixed $c \in \Delta^\circ$ and a sufficiently high mutation rate, the unique mutation equilibrium will be arbitrarily close to c. Therefore, if we were interested in finding the mutation equilibrium for a sufficiently high mutation rate, we could choose an initial point close to c and the dynamics (RMD) would converge to the asymptotically stable mutation equilibrium. The uniqueness on $(\underline{M}, \infty)$ further enables us to lower the mutation rate almost to $\underline{M}$ without losing uniqueness and asymptotic stability.

4. Mutation limits

In our previous considerations, we assumed fixed relative mutation probabilities $c \in \Delta^\circ$. In particular, certain effects could depend on the specific choice of c, e.g., if we picked c to coincide with a Nash equilibrium $x^* \in \mathcal{E}$ of the underlying game. However, we are interested in properties that are independent of the specific choice of c. To this end, we introduce the following definition:

Definition 4.1 (Mutation Limit)**.** We call a connected compact set $X \subset \mathcal{E}$ a *mutation limit*, if for all $c \in \Delta^\circ$ there is a sequence of mutation equilibria $(x^M)_{M>0} \subset \Delta$ that converges to an element of X for $M \to 0$ and X contains no proper subset with these properties. We call $x \in \Delta$ a *mutation limit point* if the singleton set $\{x\}$ is a mutation limit.

(a) General existence of mutation limits

A question that arises from the definition is that of the existence of mutation limit points. While we have shown that for any fixed $c \in \Delta^\circ$ and any mutation rate $M > 0$ there is a corresponding mutation equilibrium and therefore the Bolzano-Weierstrass theorem guarantees the existence of a limit for vanishing mutation, this limit need not be independent of the choice of c, and indeed it could be possible that there is no mutation limit at all, neither a singleton set nor otherwise. The question, therefore, is whether every game has at least one mutation limit point. To this question, we can give a negative answer, as the following example shows:

Example 4.2. Consider a two-player game with the following payoff structure:

	C_1	C_2
R_1	$1, 0$	$0, 1$
R_2	$0, 1$	$1, 0$
R_3	$0, 1$	$1, 0$

It is clear that any Nash equilibrium of the game has the form $\left(\left(\frac{1}{2}, \frac{t}{2}, \frac{1-t}{2}\right), \left(\frac{1}{2}, \frac{1}{2}\right)\right)$ with $t \in [0, 1]$, where we give the strategy of the row player first. Excluding a few special choices of $c \in \Delta^\circ$, for any generic c given as $((c_{R,1}, c_{R,2}, c_{R,3}), (c_{C,1}, c_{C,2}))$, every sequence of mutation equilibria will converge to a Nash equilibrium of the above form with $t = c_{R,2}\left(c_{R,2} + c_{R,3}\right)^{-1}$. It is therefore evident that this game has no mutation limit point, i.e., there is no Nash equilibrium that is approached by mutation equilibria for all choices $c \in \Delta^\circ$. However, for any Nash equilibrium x of the above form with $t \in (0, 1)$ there is a $c \in \Delta^\circ$ such that x is approached by a sequence of mutation equilibria. Therefore, the set of Nash equilibria is indeed a mutation limit.

In the above example, the set of all Nash equilibria turns out to be a mutation limit. However in general, the set of Nash equilibria need not be connected. In this context, the following result answers the question about the general existence of mutation limits (proven in appendix B):

Proposition 4.3. *For every* $f \in \mathcal{C}^1(U \supset \Delta, \mathbb{R}^S)$ *there is a mutation limit* $X \subset \mathcal{E}$.

Note that this result does not require that there is no intraspecies interaction, i.e., it does not require $\frac{\partial}{\partial x_{ik}} f_{ih}(x) = 0$ $(\forall i \in I, h, k \in S_i, x \in \Delta)$. In fact, the proof can be quite easily generalized to other, not necessarily replicator dynamics. From proposition 4.3, we obtain the following existence result for dynamics with only a finite number of Nash equilibria:

Corollary 4.4. *Let* $f \in \mathcal{C}^1(U \supset \Delta, \mathbb{R}^S)$ *such that the set of Nash equilibria,* $\mathcal{E}$*, is finite. Then all mutation limits are mutation limit points and there is at least one mutation limit point.*

Note that the finiteness condition is particularly important for fitness functions that are not derived from finite normal-form games.

A sufficient condition for mutation limits

We can further guarantee that regular Nash equilibria, introduced in [48], cf. also [49], are mutation limit points, where we employ the following equivalent definition, [30]:

Definition 4.5. We call a Nash equilibrium $x \in \Delta$ a *regular equilibrium* if the reduced Jacobian of (RD) at x, $D\tilde{\phi}(x)$, is invertible.

In particular, all strict Nash equilibria are regular, [49, Cor. 2.5.3].

Lemma 4.6. *Let x^* be a regular equilibrium. Then x^* is a mutation limit, i.e., for all $c \in \Delta^\circ$, there is a sequence of mutation equilibria, $(x^M)_{M>0}$, such that $x^M \to x^*$ for $M \to 0$.*

Proof. Note that $D\tilde{\phi}(x^*)$ is invertible and therefore, by the implicit function theorem, for every $c \in \Delta^\circ$, there is a continuously differentiable $\mu : (-\varepsilon, \varepsilon) \to \mathbb{R}^N$ for some $\varepsilon > 0$, such that for $M \in (-\varepsilon, \varepsilon)$ we have that $\tilde{\phi}^M(\mu(M)) = 0$. Of course, negative values of M are not interpretable as mutation rates and we consider them here only for technical reasons of differentiability at 0.

If $x^* \in \Delta^\circ$, then it is clear that we can choose ε such that $\mu([0, \varepsilon]) \subset \Delta$, and therefore a sequence of mutation equilibria $(x^M)_{M>0} \subset \Delta$ with $x^M \to x^*$ for $M \to 0$.

Suppose that $x^* \in \partial\Delta$ and for some $(i, h) \in S$ we have $x^*_{ih} = 0$. Note that μ is continuously differentiable and therefore for $M \in (-\varepsilon, \varepsilon)$,

$$\begin{aligned} 0 &= \frac{d}{dM}\phi^M_{ih}(\mu(M)) = \frac{d}{dM}\Big(\mu_{ih}(M)g_{ih}(\mu(M))\Big) + \frac{d}{dM}\Big(M(c_{ih} - \mu_{ih}(M))\Big) \\ &= g_{ih}(\mu(M))\frac{d}{dM}\mu_{ih}(M) + \mu_{ih}(M)\frac{d}{dM}g_{ih}(\mu(M)) + (c_{ih} - \mu_{ih}(M)) - M\frac{d}{dM}\mu_{ih}(M) \end{aligned}$$

and hence for $M = 0$,

$$\begin{aligned} 0 &= \frac{d}{dM}\phi^M_{ih}(\mu(M))\big|_{M=0} = g_{ih}(\mu(0))\frac{d}{dM}\mu_{ih}(0) + \mu_{ih}(0)\frac{d}{dM}g_{ih}(\mu(0)) + (c_{ih} - \mu_{ih}(0)) - 0 \\ &= g_{ih}(x^*)\frac{d}{dM}\mu_{ih}(0) + \underbrace{x^*_{ih}}_{=0}\frac{d}{dM}g_{ih}(x^*) + (c_{ih} - \underbrace{x^*_{ih}}_{=0}) = g_{ih}(x^*)\frac{d}{dM}\mu_{ih}(0) + c_{ih} \\ &> g_{ih}(x^*)\frac{d}{dM}\mu_{ih}(0)\,. \end{aligned}$$

Thus, with x^* being a Nash equilibrium, we have $g_{ih}(x^*) \leqslant 0$ and therefore $\frac{d}{dM}\mu_{ih}(0) \geqslant 0$. Because of the strict inequality, we even have $g_{ih}(x^*) < 0$ and $\frac{d}{dM}\mu_{ih}(0) > 0$. Therefore, we can choose ε such that $\mu([0, \varepsilon)) \subset \Delta$ and a sequence of mutation equilibria converging to x^*. □

Remark. It should be noted that the proof of the above result shows that there is a continuously differentiable function mapping mutation rates to mutation equilibria and that this function is unique. In other words, given a $c \in \Delta^\circ$, the sequence approaches x^* in a unique manner.

(b) Attracting Mutation Limits

Up to this point we have considered equilibria (or sets of equilibria) of (RD) such that for any $c \in \Delta^\circ$ and mutation rate $M > 0$ a mutation equilibrium of the respective (RMD) would be located arbitrarily close, depending on M. We have so far ignored the stability properties of the mutation equilibria arising nearby. If the mutation equilibrium arising nearby happens to be asymptotically stable for some mutation rate $M > 0$ and some $c \in \Delta^\circ$, then under suitable initial conditions the system will converge to a state close to the mutation limit. However, as with the notion of mutation equilibria, such behaviour of the system is mostly of interest if it does not depend on a lucky choice of c, in particular if nearby mutation equilibria turn out to be asymptotically stable for every choice of c. In this case, the mutation limit would be approximated arbitrarily close in all (RMD) only depending on $M > 0$. This idea motivates the following formal definition:

Definition 4.7 (Attracting Mutation Limit)**.** We call a mutation limit $X \subset \Delta$ *attracting* if for every $c \in \Delta^\circ$ and every sequence of mutation equilibria $(x^M)_{M>0}$ that converges to an element of X, there is $m > 0$ such that for all $M < m$, x^M is asymptotically stable. We call $x \in \Delta$ an *attracting* mutation limit point if the singleton set $\{x\}$ is an attracting mutation limit.

A sufficient condition for attracting mutation limits

It is known that if x^* is a strict Nash equilibrium, then $D\tilde{\phi}(x^*)$ has only real, strictly negative eigenvalues, e.g., [30, Lemma 1], and x^* is therefore regular and thus a mutation limit. Furthermore, we can show that x^* is an attracting mutation limit:

Lemma 4.8. *Let x^* be a strict Nash equilibrium. Then x^* is an attracting mutation limit.*

Proof. With the previous note, it is clear that x^* is a mutation limit. It remains to show that the mutation equilibria $(x^M)_{M>0}$ converging to x^* for any $c \in \Delta^\circ$ are asymptotically stable. Since all eigenvalues of the Jacobian at x^* have strictly negative real parts, and in fact are real, [30], we have that the eigenvalues of $D\tilde{\phi}(x)$ have strictly negative real parts in a neighbourhood of x^*, as the roots of a polynomial vary continuously with its coefficients, e.g., [50], and $D\tilde{\phi}$ is continuous. Therefore, in a neighbourhood of x^*, all eigenvalues of the Jacobian of $\tilde{\phi}^M$, with $D\tilde{\phi}^M(x) = D\tilde{\phi}(x) - M \cdot I$, have strictly negative real parts for any $M \geqslant 0$, and thus the x^M are asymptotically stable, e.g., [47]. □

Remark 4.9. Since the strict Nash equilibria are exactly the asymptotically stable equilibria of (RD), this ensures that all asymptotically stable equilibria are also attracting mutation limits, including evolutionary stable equilibria.

The following example shows that attracting mutation limits are not necessarily strict Nash equilibria, and hence that the concept of attracting mutation limits is also weaker than evolutionary stability:

Example 4.10. Consider the 2-by-2 matching pennies game given by the payoffs:

$$\begin{pmatrix} (1,0) & (0,1) \\ (0,1) & (1,0) \end{pmatrix}$$

The strategy profile $((\frac{1}{2}, \frac{1}{2}), (\frac{1}{2}, \frac{1}{2}))$ is a Nash equilibrium but not strict and hence not asymptotically stable. However, it is an attracting mutation limit: The eigenvalues of the Jacobian $D\tilde{\phi}$ are given by $\lambda_{1,2} = \pm\sqrt{(1-2x)^2(1-2y)^2 - 4x(1-x)y(1-y)}$. At $(\frac{1}{2}, \frac{1}{2})$, the radicand is negative and the eigenvalues purely imaginary. Hence, the radicand is negative in a neighbourhood and the eigenvalues purely imaginary. Then the eigenvalues of $D\tilde{\phi}^M$ have real part $-M$ in that neighbourhood due to remark 3.7 and for M sufficiently small all mutation equilibria are asymptotically stable with corollary 3.6, and hence $((\frac{1}{2}, \frac{1}{2}), (\frac{1}{2}, \frac{1}{2}))$ is an attracting mutation limit point. This also holds for the general matching pennies game, which we prove in a forthcoming article.

A necessary condition for attracting mutation limits

The observation that not all Nash equilibria are attracting mutation limits relies on the following:

Lemma 4.11. *Let $x^* \in \Delta$ be an attracting mutation limit. Then all eigenvalues of the Jacobian $D\tilde{\phi}(x^*)$ have nonpositive real parts.*

Proof. Suppose there is an eigenvalue of $D\tilde{\phi}(x^*)$ with a strictly positive real part. Then there is $\varepsilon > 0$ and a neighbourhood U of x^* such that $D\tilde{\phi}(x)$ has an eigenvalue λ with $\Re(\lambda) > \varepsilon$ for all $x \in U$. Let $(x^M)_{M>0}$ be a sequence of mutation equilibria converging to x^* for some $c \in \Delta^\circ$. Then there is ε' such that $x^M \in U$ for $M < \varepsilon'$. In particular, we can choose $\varepsilon' < \varepsilon$. Then the Jacobian $D\tilde{\phi}^M(x^M)$, with $D\tilde{\phi}^M(x^M) = D\tilde{\phi}(x^M) - M \cdot I$, has an eigenvalue with strictly positive real part, and x^M is not asymptotically stable, as it is not even stable, e.g., [51]. Therefore, x^* is not an attracting mutation limit. □

This result, together with the following example, then demonstrates that not all Nash equilibria are attracting mutation limits:

Example 4.12. Consider the 2-by-2 coordination game given by:

$$\begin{pmatrix} (1,1) & (0,0) \\ (0,0) & (1,1) \end{pmatrix}$$

The strategy profile $((\frac{1}{2}, \frac{1}{2}), (\frac{1}{2}, \frac{1}{2}))$ is a Nash equilibrium, but its Jacobian has eigenvalues $\frac{1}{2}$ and $-\frac{1}{2}$ and therefore it is not an attracting mutation limit.

5. Discussion

We have shown that a very simple form of mutation leads to qualitative changes in the multi-population replicator dynamics. Furthermore, these changes do not depend on the specific choice of parameters but are of a general character. Not only do mutation limits exist for all continuously differentiable fitness functions, mutation can also cause the dynamics to approximate equilibria that would not be approximated without mutation, again independently of the choice of specific mutation parameters, which is due to asymptotically stable equilibria arising close to an original equilibrium, as in the matching pennies game. The closest results to our approach that we are aware of are presented in [30], and if considered as an approximation to RD, certain aspects of RMD are clarified by those results, as indicated. The results presented here differ in that they show robustness in a system of families of approximations which are not related to perturbed normal-form game payoffs and in that they focus on the effects on the stability of equilibria, independent of the choice of the specific approximation.

With respect to periodic behaviour in biological populations it should be noted that the degree of stabilisation of RD depends on the mutation rate, resulting in a very slow approach of an asymptotically stable mutation equilibrium and seemingly periodic behaviour if mutation is low. In an empirical situation this can lead to difficulties in distinguishing dynamics with truly periodic behaviour from ones with only seemingly periodic behaviour if measuring on a (relatively) small time scale. Furthermore, in small populations stochastic effects will play a significant role. Therefore, under very low mutation, empirical findings of periodic fluctuations can be consistent with our results if measured in small populations on a small time scale, such that any stabilising effects of mutation will be more apparent in large populations on large time scales, or with sufficiently fast reproduction.

On the one hand, given the potential health impacts of even slight mutations on organisms and the fact that such mutations occur with a non-negligible probability, as mentioned earlier, and given further its role as a generator of variety on which evolutionary selection operates, it is clear that it is worth including mutation mechanisms in the study of populations, and one should expect results that deviate potentially significantly from models without mutation.

On the other hand, given that the multi-population replicator dynamics has been shown to be related to learning dynamics and that mutation-like terms have been shown to arise in formulations of Q-learning algorithms, it is worth noting that our results show that replicator-mutator dynamics have more desirable convergence properties than the pure replicator dynamics, while remaining arbitrarily close to a Nash equilibrium. Therefore, attracting mutation limits resulting from a replicator-mutator dynamics can be considered a more suitable class of dynamic solution approaches for games than the pure multi-population replicator dynamics.

As shown, attracting mutation limits do not exist for all games, and the characterization of their existence is therefore an open problem. We will address this problem partially in forthcoming results on attracting mutation limits in the matching pennies game, which can be considered a model of antagonistic coevolution. Furthermore, we have considered a specific form of mutation, and therefore the question of which properties carry over to more complicated and more realistic mutation mechanisms remains.

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A. Proof of proposition 3.10

The proof of proposition 3.10 relies on the implicit function theorem, which we restate for convenience, e.g., as in [52, Thm 3.3.1]:

Theorem A.1 (Implicit Function). *Let* $W \subset \mathbb{R}$, $X \subset \mathbb{R}^n$ *be open and let* $\rho : W \times X \to \mathbb{R}^n, (w, x) \mapsto \rho(w, x)$ *be a continuously differentiable function. Let further* $(w', x') \in W \times X$ *be such that* $\rho(w', x') = 0$ *and the* $n \times n$ *matrix* $\frac{\partial}{\partial x}\rho(w', x')$ *be invertible.*

Then there exist an open neighbourhood $W_F \subset W$ *of* w'*, an open neighbourhood* $X_F \subset X$ *of* x'*, and a continuously differentiable function* $F : W_F \to X_F$ *such that* $\forall w \in W_F : \rho(w, F(w)) = 0$*. Furthermore, for all* $(w, x) \in W_F \times X_F$ *we have that* $\rho(w, x) = 0$ *if and only if* $x = F(w)$*, i.e.,* F *is unique.*

For the proof of proposition 3.10 we will need a consequence of the implicit function theorem, based on the following statement that we can extend an implicitly defined function if the conditions of the implicit function theorem hold on the boundary of its domain:

Lemma A.2. *Let* $\rho : W \times X \to \mathbb{R}^n$ *be as given in* A.1 *and let* $R : W_R \to X_R$ *be continuously differentiable, with open and convex* $W_R \subset W$ *and open* $X_R \subset X$*, such that:*

i) $\forall v \in W_R : \rho(v, R(v)) = 0$*;*
ii) $\forall (v, x) \in W_R \times X_R : \ \rho(v, x) = 0 \Leftrightarrow x = R(v)$*.*

If for some sequence $(v_n)_{n\in\mathbb{N}} \subset W_R$ *with* $v_n \to v' \in \partial W_R \cap W$ *and an accumulation point* $x' \in X$ *of* $(R(v_n))_{n\in\mathbb{N}}$*, the matrix* $\frac{\partial}{\partial x}\rho(v', x')$ *is invertible, then there is a unique continuously differentiable extension of* R *with the above properties whose domain is open and a proper superset of* W_R*. In particular,* $(R(v_n))_{n\in\mathbb{N}}$ *is convergent with limit* x'*.*

Proof. Let $(v_n)_{n\in\mathbb{N}} \subset W_R$ with $v_n \to v' \in \partial W_R \cap W$ and let $x' \in X$ be an accumulation point of $(R(v_n))_{n\in\mathbb{N}}$, such that the matrix $\frac{\partial}{\partial x}\rho(v', x')$ is invertible. Due to the continuity of ρ on $W \times X$, we have that $\rho(v', x') = 0$. With the implicit function theorem, there are open neighbourhoods $W' \subset W$ of v', where we can require W' to be convex, and $X' \subset X$ of x' and a unique continuously differentiable function $S : W' \to X'$ with the corresponding properties i) and ii).

We will show that there is N such that $(R(v_n))_{n\geqslant N} \subset X'$: As x' is an accumulation point of $(R(v_n))_{n\in\mathbb{N}}$, there are infinitely many $n \in \mathbb{N}$ with $R(v_n) \in X'$, in particular let $R(v_N) \in X'$. Note that we can assume $(v_n)_{n\geqslant N} \subset W'$ as $v' \in W'$ is the limit of that sequence. Assume that there is some $N' > N$ with $R(v_{N'}) \notin X'$ and let N' be minimal. W.l.o.g. let $N' = N + 1$ and define $v : [0, 1] \to W', t \mapsto (1 - t)v_N + tv_{N'}$. Then $v([0, 1]) \subset W'$ due to convexity. Consider that $R(v_N) \in X'$, with X' open. Therefore, there is some $\varepsilon > 0$ with $R(v([0, \varepsilon])) \subset X'$. However, with our assumption, $R(v(1)) = R(v_{N'}) \notin X'$. Then, with the complement of X' being closed, there is a minimal $\bar{t}$ such that $R(v(\bar{t})) \notin X'$. Then $R \circ v = S \circ v$ on $[0, \bar{t})$, but due to their continuity we then also have $R(v(\bar{t})) = S(v(\bar{t}))$ and thus $R(v(\bar{t})) \in X'$, in contradiction to $R(v(\bar{t})) \notin X'$. Thus, $R(v_{N'}) = R(v(1)) \in X'$, in contradiction to $R(v_{N'}) \notin X'$. Overall, we then have $(R(v_n))_{n\geqslant N} \subset X'$, and further $R([v_N, v')) \subset X'$ (assuming $v_N < v'$). This implies that $R = S$ on $W_R \cap W'$ and $T := R \cup S$ is a proper, continuously differentiable extension of R, satisfying properties i) and ii). In particular, due to $(R(v_n))_{n\geqslant N} = (T(v_n))_{n\geqslant N}$, $(R(v_n))_{n\in\mathbb{N}}$ is convergent with limit x'. ☐

The following lemma states that there is an implicitly defined function whose domain is such that the points at the boundary do not satisfy the conditions of the implicit function theorem:

Lemma A.3. *Let* $\rho : W \times X \to \mathbb{R}^n$ *be as given in* A.1 *and* $(w, x^w) \in W \times X$ *such that* $\rho(w, x^w) = 0$ *and the matrix* $\frac{\partial}{\partial x}\rho(w, x^w)$ *is invertible. Then there exist open neighbourhoods* $W^* \subset W$ *of* w*, with* W^* *convex, and* $X^* \subset X$ *of* x^w*, and a continuously differentiable function* $R^* : W^* \to X^*$ *such that:*

i) $\forall v \in W^* : \rho(v, R^*(v)) = 0$*;*

ii) $\forall (v, x) \in W^* \times X^* : \rho(v, x) = 0 \Leftrightarrow x = R^*(v)$;
iii) for all $(v_n)_{n\in\mathbb{N}} \subset W^*$ *with* $v_n \to v' \in \partial W^* \cap W$ *and every accumulation point* $x' \in X$ *of* $(R^*(v_n))_{n\in\mathbb{N}}$, *the matrix* $\frac{\partial}{\partial x}\rho(v', x')$ *is singular.*

In particular, R^* *is a maximally defined such function.*

Proof. Let $\mathcal{R}$ be the set of all continuously differentiable functions $R_\alpha : W_\alpha \to X_\alpha$, with $W_\alpha \subset W$ convex and $X_\alpha \subset X$ being open neighbourhoods of w and x^w, respectively, such that R_α satisfies i) and ii). Due to ρ being continuously differentiable, $\frac{\partial}{\partial x}\rho$ is invertible in a convex, open neighbourhood of (w, x^w). With the implicit function theorem, $\mathcal{R}$ is not empty. We define a partial order on $\mathcal{R}$ by the set inclusion on the graphs of the functions $R_\alpha \in \mathcal{R}$.

Let $\mathcal{O}$ be a non-empty completely ordered chain in $\mathcal{R}$. Consider the function R' defined by the graph:

$$\Gamma(R') = \bigcup_{R_\alpha \in \mathcal{O}} \{(v, R_\alpha(v)) \mid v \in W_\alpha\}$$

Then $W' = \bigcup_{R_\alpha \in \mathcal{O}} W_\alpha \subset W$ and $X' = \bigcup_{R_\alpha \in \mathcal{O}} X_\alpha \subset X$ are open neighbourhoods of w and x^w and $R' : W' \to X'$ is a continuously differentiable function. Furthermore, $\{W_\alpha \mid R_\alpha \in \mathcal{O}\}$ is completely ordered by set inclusion as well and therefore, W' is convex. It is clear that R' satisfies i) as all R_α satisfy i). Let $(v, x) \in W' \times X'$. Then there is $R_\alpha \in \mathcal{O}$ with $v \in W_\alpha$, $x \in X_\alpha$, and $R'(v) = R_\alpha(v)$. Then, as R_α satisfies ii), we have $\rho(v, x) = 0 \Leftrightarrow x = R_\alpha(v) = R'(v)$, and thus R' satisfies ii). Therefore, $R' \in \mathcal{R}$, and with Zorn's Lemma, $\mathcal{R}$ contains a maximal element $R^* : W^* \to X^*$, such that R^* satisfies i) and ii).

For iii), let $(v_n)_{n\in\mathbb{N}} \subset W^*$ with $v_n \to v' \in \partial W^* \cap W$ and let $x' \in X$ be an accumulation point of $(R^*(v_n))_{n\in\mathbb{N}}$. Assume that the matrix $\frac{\partial}{\partial x}\rho(v', x')$ is invertible. With the previous lemma there is a proper extension of R^* and R^* is not maximal, a contradiction. Thus, $\frac{\partial}{\partial x}\rho(v', x')$ is singular. ☐

In order to apply the above lemma, for $M > 0$, we rewrite (RMD) as

$$\rho : \mathbb{R} \times X \to \mathbb{R}^S, (w, x) \mapsto w\phi(x) + (c - x) \tag{A 1}$$

with $w = M^{-1}$. It is clear that $\rho(M^{-1}, x) = M^{-1}\phi^M(x)$ and therefore $\rho(M^{-1}, x) = 0 \Leftrightarrow \phi^M(x) = 0$ and that ρ is continuously differentiable on $\mathbb{R} \times X$ with some $X \supset \Delta$ open and bounded, depending on ϕ. Then we obtain lemma 3.9 as a corollary:

Corollary A.4. *Let* $c \in \Delta^\circ$ *and* $\underline{M}$ *be as in lemma 3.8. Let* x^M *be a mutation equilibrium for some* $M > \underline{M}$. *Then there is a unique function* $\mathcal{M} : (\underline{M}, \infty) \to \Delta$ *such that* $\mathcal{M}(M) = x^M$ *and for all* $m \in (\underline{M}, \infty)$, $\mathcal{M}(m)$ *is a mutation equilibrium for* m. *In particular,* $\mathcal{M}$ *is continuously differentiable and* $\mathcal{M}(m) \xrightarrow{m\to\infty} c$.

Proof. Consider that for $m > \underline{M}$, $D\phi^m$ is invertible everywhere on Δ due to lemma 3.8, and that for $w = m^{-1}$ with ρ from (A 1), the matrix $\frac{\partial}{\partial x}\rho(w, x)$ is invertible whenever $D\phi^m(x)$ is. Then let $\underline{w} = \underline{M}^{-1}$ and $w = M^{-1}$ for some $M > \underline{M}$. Then applying the previous lemma to w, x^M and ρ yields a continuously differentiable function $R : W \to \Delta$ with $W \subset \mathbb{R}$ and $w \in W$. Furthermore, the previous lemma guarantees that $[0, \underline{w}) \subset W$ because $\frac{\partial}{\partial x}\rho(v, x)$ is invertible $\forall v \in [0, \underline{w}), x \in \Delta$. Thus, $\mathcal{M} : (\underline{M}, \infty) \to \Delta$ with $m \mapsto R(m^{-1})$ is continuously differentiable and is as desired. ☐

With this we can prove proposition 3.10:

Proposition A.5 (3.10). *Let* $c \in \Delta^\circ$ *and* $\underline{M}$ *as in lemma 3.8. For all* $M > \underline{M}$, *the replicator-mutator dynamics* (RMD) *has a unique mutation equilibrium. The unique map* $\mathcal{M} : M \mapsto x^M$ *is continuously differentiable on* $(\underline{M}, \infty)$.

Proof. As ϕ is Lipschitz, let L_ϕ be the best Lipschitz constant for ϕ. Since ϕ is differentiable and Δ is convex, we further have that $L_\phi = \|D\phi\|_{\infty,\Delta} := \sup_{x\in\Delta} \|D\phi(x)\| \geqslant \underline{M}$ with $\underline{M}$ from lemma

3.8. Choose $M' > L_\phi$ and consider for $c \in \Delta^\circ$ and some $s > 0$ the function $F_{M',c} : \Delta \to \Delta$ with $[F_{M',c}(x)]_{ih} = x_{ih} + s\left(\phi_{ih}(x) + M'(c_{ih} - x_{ih})\right)$. Then, we have that

$$[F_{M',c}(x)]_{ih} - [F_{M',c}(y)]_{ih} = (1 - sM')(x_{ih} - y_{ih}) + s\left(\phi_{ih}(x) - \phi_{ih}(y)\right)$$

and thus

$$\begin{aligned}\|F_{M',c}(x) - F_{M',c}(y)\| &\leqslant |1 - sM'|\|x - y\| + s\|\phi(x) - \phi(y)\| \\ &\leqslant |1 - sM'|\|x - y\| + sL_\phi\|x - y\| = (|1 - sM'| + sL_\phi)\|x - y\|\,.\end{aligned}$$

Choosing s such that $sM' \leqslant 1$, we have that:

$$|1 - sM'| + sL_\phi = 1 - sM' + sL_\phi = 1 + s(L_\phi - M') < 1$$

Hence, $F_{M',c}$ is a contractive mapping and has a unique fixed point $x^{M'} \in \Delta^\circ$. Then every function $\mathcal{M}$ from corollary A.4 satisfies $\mathcal{M}(M') = x^{M'}$ and thus all such functions are identical, yielding the uniqueness of mutation equilibria for all $M > \underline{M}$. ☐

B. Proof of proposition 4.3

In order to prove proposition 4.3, we need to extend (RMD) slightly, such that we can allow more general mutation to occur. Recall that $g_{ih}(x) = f_{ih}(x) - \bar{f}_i(x)$ and that then $\mathcal{E} = \{x \in \Delta \mid g(x) \leqslant 0\}$ is the set of Nash equilibria, where the inequality is component-wise. Then let $H = \mathcal{C}^1(\Delta, \mathbb{R}^S_{>0})$, and define for $c \in H$, $M > 0$:

$$[F_{M,c}(x)]_{ih} = x_{ih} + s\left(x_{ih} g_{ih}(x) + M\left(c_{ih}(x) - x_{ih}\textstyle\sum_{k \leqslant n_i} c_{ik}(x)\right)\right)$$

where $i \in I$, $h \in S_i$. Note that for all $s > 0$, the fixed points of $F_{M,c}$ are the stationary points of a suitably generalized (RMD). In particular, if $c \in H$ is constant on Δ, then the fixed points are exactly the mutation equilibria of (RMD) for a suitably chosen $\tilde{M}$. It is clear that for a choice of $c \in H$, we can choose $s > 0$ such that for all $M \in (0, \varepsilon_s)$, we have $F_{M,c}(\Delta) \subset \Delta$ and thus the set of fixed points is non-empty. Therefore, we assume a suitable choice of $s > 0$ (possibly depending on c). For convenience, let us denote by $\mathscr{F}(F_{M,c})$ the set of fixed points of $F_{M,c}$ for $c \in H$ and $M > 0$:

$$\mathscr{F}(F_{M,c}) = \{x \in \Delta \mid F_{M,c}(x) = x\}.$$

From the definition of a mutation limit, we extract the main property and say that a set $X \subset \Delta$ has the property (A) if

(A) for all $c \in \Delta^\circ$, there is a sequence of mutation equilibria $(x^M)_{M>0} \subset \Delta$ that converges to an element of X.

We extend this notion to $F_{M,c}$ and say that a set $X \subset \Delta$ has the property (A') if

(A') for all $c \in H$ and open $U \supset X$, there is $M > 0$ such that $\mathscr{F}(F_{M,c}) \cap U \neq \varnothing$.

Remark. It is clear that a set X has the property (A') if and only if for every $c \in H$ there is a sequence $(x^M)_{M>0} \subset \Delta$ such that $(x^M)_{M>0}$ converges to an element of X and every x^M in the sequence satisfies $x^M \in \mathscr{F}(F_{M,c})$. With this it is also clear that a set has the property (A) if it has property (A'), due to $c \in \Delta^\circ$ being equivalent to a constant function in H.

The proof of proposition 4.3 will proceed as follows: We first show that $\mathcal{E}$ has the property (A'). Next, we show that a set with the property (A') contains a minimal set with that property, and that an analog but slightly modified result holds for the property (A). We then show that a minimal set with the property (A') is connected, based on a proof by Kinoshita [53]. Thus, we have that $\mathcal{E}$ contains a minimal set with the property (A'), which must be contained in a connected component of $\mathcal{E}$. Finally this set is connected and in particular has the property (A) and hence contains a minimal connected set with the property (A), proving proposition 4.3.

Existence. We show first that any minimal set with the property (A') must be contained in $\mathcal{E}$:

Lemma B.1. *Let $X \subset \Delta$ be minimal with the property (A'). Then $X \subset \mathcal{E}$ and $\mathcal{E}$ has the property (A').*

Proof. Assume that $X \not\subset \mathcal{E}$. Let $c \in H$ and $(M_n)_{n\in\mathbb{N}} \subset \mathbb{R}_{>0}$ be a null sequence, and $(x^{M_n})_{n\in\mathbb{N}} \subset \Delta$ convergent with limit x^* with $x^{M_n} \in \mathscr{F}(F_{M_n,c})$ for all $n \in \mathbb{N}$. From our earlier note on the possibility of a constant choice of $s > 0$ for all $n \in \mathbb{N}$, and from the continuity of g and c, we have that for all $i \in I$, $h \in S_i$, $x^*_{ih} g_{ih}(x^*) = 0$ holds.

We now show that $x^* \in \mathcal{E}$: If $x^* \in \Delta^\circ$, then for all $i \in I$, $h \in S_i$, $x^*_{ih} g_{ih}(x^*) = 0$ implies $g_{ih}(x^*) = 0$, i.e., $x^* \in \mathcal{E}$. If $x^* \in \partial\Delta$, then let some $(i,h) \in S$ be such that $x^*_{ih} = 0$, and let $\tilde{c}_i = \sup\left\{\sum_{k\leqslant n_i} c_{ik}(x) \mid x \in \Delta\right\}$. Then $\tilde{c}_i < \infty$ and for $M > 0$:

$$\begin{aligned} x^M_{ih} = [F_{M,c}(x^M)]_{ih} &= x^M_{ih} + s\left(x^M_{ih} g_{ih}(x^M) + M\left(c_{ih}(x^M) - x^M_{ih}\sum_{k\leqslant n_i} c_{ik}(x^M)\right)\right) \\ &> x^M_{ih} + s\left(x^M_{ih} g_{ih}(x^M) - M x^M_{ih}\sum_{k\leqslant n_i} c_{ik}(x^M)\right) \geqslant x^M_{ih} + s x^M_{ih}\left(g_{ih}(x^M) - M\tilde{c}_i\right) \end{aligned}$$

Therefore, we have for all $M > 0$:

$$0 > s x^M_{ih}\left(g_{ih}(x^M) - M\tilde{c}_i\right) \qquad \Leftrightarrow \qquad 0 > g_{ih}(x^M) - M\tilde{c}_i \qquad \Leftrightarrow \qquad M\tilde{c}_i > g_{ih}(x^M)$$

Therefore, with $M \to 0$, we have $g_{ih}(x^*) \leqslant 0$, and overall $x^* \in \mathcal{E}$. Thus $X \cap \mathcal{E}$ has the property (A') and X is not minimal, a contradiction. From $x^* \in \mathcal{E}$, it is clear that $\mathcal{E}$ has the property (A'). □

Minimality. We first show that the existence of a set with the property (A') implies the existence of a minimal such set, where the proof is fairly standard and adapted from [54, Thm 7.3]:

Lemma B.2. *Let a compact set $X \subset \Delta$ have the property (A'). Then it contains a minimal compact set with the property (A').*

Proof. The proof is based on Zorn's lemma. Let C be the set of compact subsets of X with the property (A'), i.e., $C = \{K \subset X \mid K \neq \varnothing$ and K is compact and has the property $(A')\}$, and order C by reverse inclusion $\supset$. Let $O \subset C$ be completely ordered. Then O has the finite intersection property, as it is completely ordered by reverse inclusion and its elements are compact. Therefore, $K_\infty := \bigcap O \neq \varnothing$ and K_∞ is compact.

It remains to show that K_∞ has the property (A'): Assume K_∞ does not have the property (A'). Then there is a $c \in H$ and an open neighbourhood V of K_∞ such that no $F_{M,c}$ $(M > 0)$ has a fixed point in V. For $L \in O$, we have $L \not\subset V$ because L has the property (A'). Then $O' := \{L \backslash V : L \in O\}$ is a completely ordered collection of compact sets (L is compact and V is open) with the finite intersection property, inherited from the reverse inclusion ordering of O. Therefore, it has a nonempty intersection $K'_\infty \subset K_\infty \subset V$ but $K'_\infty \cap V = \varnothing$, which is a contradiction. Thus, K_∞ has the property (A') and therefore $K_\infty \in C$ is an upper bound of O. With Zorn's lemma then, C has a maximal element, which is a minimal compact subset of X with the property (A'). □

For the existence of a mutation limit we will have to make a similar step, however preserving connectedness:

Lemma B.3. *Let a connected compact set $X \subset \Delta$ have the property (A). Then it contains a minimal connected compact set with the property (A).*

Proof. Let C be the set of all compact connected (non-empty) subsets of X with the property (A), partially ordered by $\supset$ and O a completely ordered chain in C. Then $K_\infty = \bigcap_{K\in O} K$ is non-empty, compact and has the property (A) by an argument completely analogous to the previous lemma.

It remains to show that K_∞ is connected: Assume that K_∞ is not connected. Then, there are open disjoint sets U_1, U_2, with $K_\infty \subset U_1 \cup U_2 =: U$ and $K_\infty \cap U_1 \neq \varnothing$, $K_\infty \cap U_2 \neq \varnothing$, and U open in X. X and all $K \in O$ are compact and, with X being Hausdorff, also closed. Thus $X\backslash K$ is open in X for $K \in O$. Then, with $\bigcup_{K\in O} X\backslash K = X\backslash \bigcap_{K\in O} K = X\backslash K_\infty$, we have that $\{U\} \cup \{X\backslash K | K \in O\}$ is an open cover of X, and there is a finite subcover $\{U\} \cup \{X\backslash K_i | K_i \in O, 1 \leqslant i \leqslant n\}$, as X is compact. Thus $X = U \cup \bigcup_{1\leqslant i\leqslant n} X\backslash K_i = U \cup X\backslash \bigcap_{1\leqslant i\leqslant n} K_i$. As O is completely ordered by inclusion, we can assume that $K_i \supset K_n$ $(1 \leqslant i \leqslant n)$ and we have that $X = U \cup X\backslash K_n$. Thus $K_n \subset U = U_1 \cup U_2$, and hence K_n is not connected, a contradiction. Therefore, K_∞ is connected and $K_\infty \in C$. With Zorn's lemma the statement of the lemma follows. ☐

Connectedness. We gain connectedness as a necessary property of minimal sets with the property (A'), where the main idea of the proof is based on a proof by Kinoshita [53] and relies on the "convexity" of H:

Lemma B.4. *If $K \subset \Delta$ has the property (A') and $K = (K_1 \cup \ldots \cup K_s)$ with the K_j disjoint and compact, then some K_j has the property (A'). If K is minimal with the property (A'), then K is connected.*

Proof. Let $K \subset \Delta$ have property (A') and $K = K_1 \cup \ldots \cup K_s$ with the K_j disjoint and compact. Assume that no K_j has the property (A'). Then there are $c_1, \ldots, c_s \in H$ and neighbourhoods $U_1, \ldots, U_s$ of $K_1, \ldots, K_s$ with disjoint closures such that for all $M > 0$, $\mathscr{F}(F_{M,c_j}) \cap U_j = \varnothing$. Let further $V_1, \ldots, V_s$ be strictly smaller neighbourhoods, i.e., $\overline{V}_j \subsetneq U_j$, and let U_0 be a neighbourhood of $\Delta\backslash(U_1 \cup \ldots \cup U_s)$ whose closure is disjoint from the $V_1, \ldots, V_s$, and c_0 any function in H. Then $\{U_0, U_1, \ldots, U_s\}$ is an open cover of Δ and with Δ being a compact subset of a topological vector space, there is a C^∞-partition of unity $\pi_0, \pi_1, \ldots, \pi_s$ such that $\pi_j(x) = 0$ $(\forall x \in \Delta\backslash U_j)$, and $\sum_{j=0}^{s} \pi_j(x) = 1$ $(\forall x \in \Delta)$, e.g., [54, Thm 6.2]. The convex combination, $\bar{c}$, with $\bar{c} : x \mapsto \sum_{j=0}^{s} \pi_j(x) c_j(x)$, is an element of H. Considering $F_{M,\bar{c}}$, we then have that $F_{M,\bar{c}}(x) = F_{M,c_j}(x)$ for $x \in V_j$. Thus $\mathscr{F}(F_{M,\bar{c}}) \cap V_j = \varnothing$ for $1 \leqslant j \leqslant s$ for all $M > 0$. Therefore, $F_{M,\bar{c}}$ has no fixed points in $(V_1 \cup \ldots \cup V_s) \supset K$ for any $M > 0$. This is a contradiction to the assumption that K has the property (A'). In particular, if K is minimal, then K is connected. ☐

Overall, this proves the following:

Proposition B.5. *There is a mutation limit $X \subset \mathcal{E}$.*

Proof. With lemma B.1, $\mathcal{E}$ has the property (A'). With $\mathcal{E}$ being compact due to $g \in \mathcal{C}(\Delta, \mathbb{R}^S)$ and $\mathcal{E} \subset \Delta$, and with lemma B.2, there is a minimal compact set $X' \subset \mathcal{E}$ with the property (A'). Furthermore, with lemma B.4, X' is connected. With the property (A'), X' also has the property (A). With lemma B.3, X' contains a minimal connected compact subset $X \subset X'$ with the property (A). By definition, X is a mutation limit. ☐