

# The Evolution of Populations using Local Replicator Dynamics <sup>1</sup>

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## Abstract

The interaction of Game Theory and Biology led to Evolutionary Game Theory. One of the key issues in Evolutionary Game Theory is to examine how a species develops from generation to generation. The species consists of different types of individuals. Interactions of these individuals generate offspring of the very same type as the "mother". The numbers of offspring that result from each interaction depend on the types that meet. As such the population distribution over the different types will change from one generation to the next. In the "classical" model every mother will mate with a random individual from the current population, assuming that all types are well mixed. In this thesis we examine what happens if such mixing does not occur and mothers only interact with individuals from their direct neighbourhood.

## 1 Introduction

Evolutionary Game Theory originates from the early 1970's. Maynard Smith and Price have started with analysing the behaviour of animals [2]. This research led to the "classical" model where every individual animal will interact with a random individual from the same types.

In the classical model each individual in the population mates with a random individual of the same population. How many offspring one individual bears depends on the fitness matrix. That individual is called the "mother". All individuals of a population are hermaphrodite in behaviour. A hermaphrodite in behaviour means that one individual, the "mother", mates with a random individual in the population, the "father". This means that each individual can act like a mother and a father, like a hermaphrodite.

The fitness matrix tells how many offspring any combination of mother-father gets, where the mother as

well as the father can be any type of individual in the species. The entry (type of mother, type of father) in the fitness matrix gives the number of offspring of the mother. All these children will be of the same type as the mother.

The next generation of a species consists of all the children of the current generation. The numbers of children for each of the different types will determine the composition of the new generation. This composition can be represented by the fractions of the different types of individuals among the species. The vector of these fractions is called the population distribution. This population distribution will change from generation to generation and the question arises whether or not it will stabilize in the long run.

When the composition of a species does not change anymore and can resist small fluctuations, the species is said to be evolutionary stable. This means that the population distributes according to an Evolutionary Stable Strategy (ESS).

In this biological setting the ESS replaces the Nash equilibrium [3] known from Game Theory. The Nash equilibrium states that if the composition of a population is stable, then all existing types in the population are equally fit (in terms of the payoff from the fitness matrix) and they are at least as fit as the types that have fraction 0. The ESS adds to this a stability assumption that implies that any fluctuation in the population distribution will automatically disappear again. Therefore an ESS is always a Nash equilibrium, but not all Nash equilibria are evolutionary stable. Unfortunately an ESS does not always exist.

For generating the next generation the classical model uses replicator dynamics at a global level, from now on referred to as Global Replicator Dynamics (GRD). GRD calculates the offspring of a population, assuming that all individuals interact with each other. But do individuals interact with all other individuals in a large population? Take, for example, the behaviour of human beings: people with all kinds of different backgrounds are not spread evenly over the whole country. At the same time people mainly interact with those living in their immediate neighbourhoods. This does not mean that the composition of the total

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population is different, but the individuals are just not well-mixed.

In this thesis the interaction of individuals in a population on local level is the point of focus and so the research question is: *How does a population evolve when applying Local Replicator Dynamics (LRD) compared to GRD?*

This idea developed thinking about the interaction of cells in a carcinogenic tissue. A model for LRD is worked out in this thesis. But it may be applied to other areas as well. The model on LRD is developed in section 3. The experiments show the differences when applying LRD instead of GRD, section 4, and are further discussed in section 5. Section 6 concludes the work of this thesis and suggests some extensions for further study.

## 2 Cell structures

The interaction of individuals can be interpreted in various ways. One could be the interaction between cells in a human body. Cell biologists, or briefly biologists, are interested in the way cells interact with each other, if there is any interaction. Biologists know that some types of cells do interact with each other and other types, while some types do not.

Relevant study about interactions between cells dates back from 1997. Tomlinson and Bodmer focused on the interactions between different genotypes of cancer cells (Tomlinson) [6], and developed a game-theory model where cells can have one of two possible genotypes [5]. Instead of generalizing the idea of cell interaction, several researchers extended this model, by including more detailed aspects like metabolism, e.g. see Mansury et al [1].

In this thesis the goal is to visualize the evolution of a population based on the local interaction of cells only, thus to create a general model. Therefore studying the evolution of cooperation appeared to be fundamental. The thesis about the evolution of cooperation in a spatial prisoner's dilemma [4] gave insight in how cells could interact at a local level. The prisoners in this dilemma can be cooperators or defectors, depending on the values from the payoff matrix. The payoff matrix has to fulfill several rules to create such a dilemma. Since this dilemma appears for one generation at a time, the beginnings from this evolution of cooperation are useful for this study. Cooperators and defectors could be seen as two different types of individuals in a population. The simulation of new generations of a certain population with these two types of individuals shows remarkable interactions between the cooperators and the defectors. This behaviour depends on the values

of the fitness matrix. In this thesis the fitness matrix will be a fundamental component in the model. This will be explained in the next section.

## 3 Model of Local Replicator Dynamics

A model of the interaction between individuals at a local level can be split into a few components. Subsection 3.1 is about the representation of the complete population. Crucial for the model are the fitness matrix and the neighbourhood at local level, subsection 3.2. These components together enables to generate new populations from a given population as described in subsection 3.3.

### 3.1 Population

The advantage of applying GRD lies in its assumption that all types are, and stay, equally divided in a population. Equally divided means that all individuals that belong to the same type are placed randomly with equal chance, for all types in that population. Because of this assumption, the local environment is not significant.

LRD on the other hand depends on the local environment, so this aspect is important. The work on evolution of cooperation shows the interaction between prisoners in the form of a lattice with squares, where each square represents a prisoner. Each prisoner interacts with its direct neighbour, de four prisoners that abut to the sides of the square. This is no problem for this case but if a prisoner would interact with more neighbours, a problem appears. The problem is about the prisoners that abut on to the corner of a prisoners' square.

The distance to the center of a corner prisoner is larger

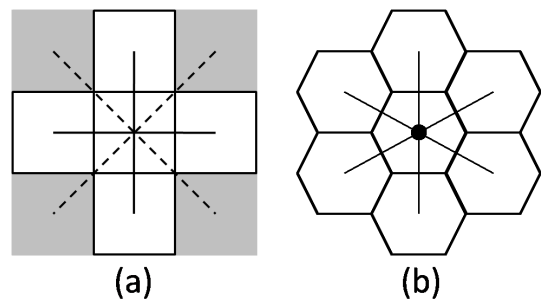


Figure 1: Difference in distances: (a) squared lattice (b) hexagonal lattice

than the distance to the center of a prisoner that abuts to the side, as shown in figure 1(a).

To avoid this problem the squared lattice is replaced by a hexagonal lattice, a lattice composed of hexagons.

Figure 1(b) shows that transitions to all direct neighbours are equal. There are no neighbours at the corners of a hexagon, only at the sides.

Since the lattice is a squared two-dimensional flat surface, some Periodic Boundary Conditions (PBC's) are defined. The hexagons that lie at a boundary of the lattice would have less neighbours. This would give a new problem or new exceptions but that is not desirable. The PBC's solve this problem by connecting the East and West sides of the lattice and the North and South side. This way the lattice turns into a torus. A torus is a surface of revolution and has the form of a doughnut.

The total number of individuals in the population remains constant during the whole process.

### 3.2 Requirements

The number of offspring any individual gets is fundamental to generate the next generation of a certain population. The two important requirements to calculate the number of offspring are the fitness-matrix and the local neighbourhood.

Each couple of individuals, a father and a mother, bears a certain number of offspring. These numbers of offspring can be referred to as the fitnessvalue for the type of the mother, that meets the type of the father.

Table 1 represents the structure of the fitness matrix in tabular form, where the numbers 1, 2, ...,  $N$  are the different types within the population. It clarifies how the matrix should be read. The rows represent the types

	1	2	...	$N$
1	(1, 1)	(1, 2)	...	(1, $N$ )
2	(2, 1)	(2, 2)	...	(2, $N$ )
$\vdots$	$\vdots$	$\vdots$	$\ddots$	$\vdots$
$N$	( $N$ , 1)	( $N$ , 2)	...	( $N$ , $N$ )

Table 1: Fitness matrix for  $N$  types.

of the mother, the columns are the father types. So if there is a population with seven types and the mother is an individual of type 3 and the father of type 5. Then the mother will get the number of offspring that corresponds to the value of entry (3, 5) in the fitness matrix. For convenient use the values in the matrix are zero or natural numbers.

How the neighbourhood of an individual using LRD is structured, is of big influence to calculate the number of offspring for the mother. For generality and because of the choice of the hexagonal lattice, each mother has six direct neighbours. But the mother can be influenced by more individuals than only the direct neighbours. Figure

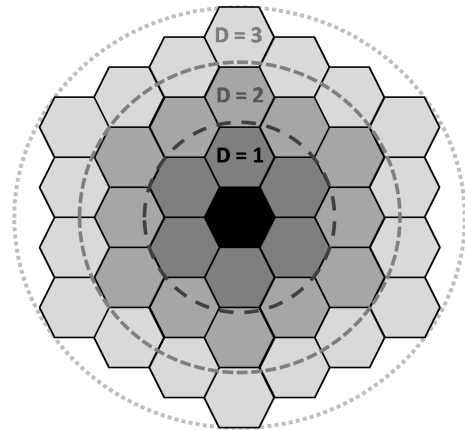


Figure 2: Neighbours at distance  $D$

2 clarifies that individuals can be influenced by other individuals within a certain distance  $D$ .

As the figure shows, the direct neighbours have distance 1. Every further 'ring' of neighbours has six neighbours more, as shown in table 2.

Distance	Number of neighbours
1	6
2	12
3	18
$\vdots$	$\vdots$
$D$	$6 \times D$

Table 2: Number of neighbours depend on the distance

### 3.3 Generations

The composition of the next generation can be divided in two parts. Beginning with the bearing of children by the mother individual after mating with a random neighbours called the father, followed by translating the number of offspring back to the original amount of individuals.

#### CALCULATING OFFSPRING

Each individual in the population acts as a mother once and each mother has a set of neighbours  $F_m$ . Those neighbours act like fathers. The mother mates with a random father,  $f \in F_m$ , and she gets  $x$  children, which inherit the type of the mother ( $m$ ). The number  $x$  depends on the fitness matrix as discussed in previous section. The corresponding value of entry (type of mother, type of father) in the fitness matrix is the value for  $x$ .

The expected offspring for the mother is given by:

$$O(m, F_m) = \frac{\sum_{f \in F_m} A(m, f)}{\|F_m\|} \quad (1)$$

This equation uses the matrix from table 1, named matrix  $A$ . The type of the mother and the set of neighbours are the input for the offspring equation. Thus the number of offspring per individual is an expected number. Instead of working with the expected numbers, one could also work with the realized number from the random draw. This is to be explored in the future, see section 6.

TRANSLATING

All children have a certain number of offspring from the same type as the mother. Since all entries in the fitness matrix may be different, the individuals are not equally divided over the hexagons. By comparing the offspring values for different types in neighbouring hexagon positions, the types for the hexagons (mothers) have to be calculated for the new generation.

For each type that occurs in the neighbourhood within distance  $D$  of an individual, the number of offspring of that type in that neighbourhood is added up together with the number of the mother. The type with the highest number of offspring in this neighbourhood becomes the new type of the mother in the central hexagons of this neighbourhood for the next generation.

In this translation the number of offspring from the mother could be increased by a certain factor. The original type obtains a higher weight, and it is more difficult to take over for the other types. The translation, like the calculation of the offspring, occurs for all individuals simultaneously and the hexagons are set to the type the individual obtains at the end of the translation. All hexagons represent one individual again as the new generation is formed.

Now the next generation can be created. But first a small example for the generation process.

EXAMPLE

A population exists of three types: 1, 2 and 3. Figure

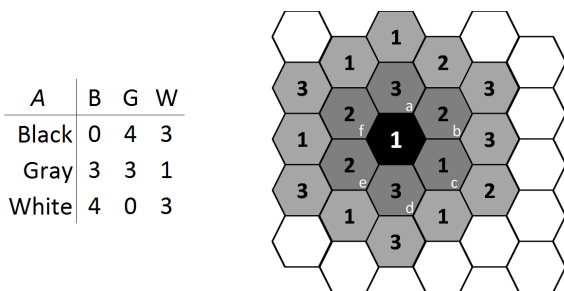


Figure 3: Fitness matrix  $A$  and population

3 shows the corresponding fitness matrix  $A$  for these types in this population. The same figure shows the actual population where the hexagons that represent the individuals that are relevant in this example are the numbered ones. The numbers indicate to what type the individual belongs. The center hexagon is the mother individual that is central in this example.

The offspring value for the mother depends on the direct neighbours:  $a, b, c, d, e$  and  $f$ . These neighbours form the set  $F$ .

The equations below show the calculation for the offspring value for the mother individual in detail.

$$\begin{aligned} O(1, F) &= \frac{\sum_{f \in F} A(1, f)}{A(1,3)+A(1,2)+A(1,1)+A(1,3)+A(1,2)+A(1,2)} \\ &= \frac{1}{6} * A(1, 1) + \frac{1}{2} * A(1, 2) + \frac{1}{3} * A(1, 3) \\ &= 1\frac{2}{3} \end{aligned}$$

Table 3 shows the results of the same calculation for the individuals that belong to the set  $F$ . The new type of the mother is the goal here, so there are no more offspring calculations needed.

The required offspring calculations are done now,

$F$	Type	Calculation	Offspring
$a$	3	$\frac{1}{2}(3, 1) + \frac{1}{2} * (3, 2)$	2
$b$	2	$\frac{1}{3}(2, 1) + \frac{1}{6} * (2, 2) + \frac{1}{2} * (2, 3)$	2
$c$	1	$\frac{1}{3}(1, 1) + \frac{1}{3} * (1, 2) + \frac{1}{3} * (1, 3)$	$2\frac{1}{3}$
$d$	3	$\frac{1}{3}(3, 1) + \frac{1}{6} * (3, 2) + \frac{1}{6} * (3, 3)$	$1\frac{1}{6}$
$e$	2	$\frac{1}{2}(2, 1) + \frac{1}{6} * (2, 2) + \frac{1}{3} * (2, 3)$	$2\frac{1}{3}$
$f$	2	$\frac{1}{2}(2, 1) + \frac{1}{6} * (2, 2) + \frac{1}{3} * (2, 3)$	$2\frac{1}{3}$

Table 3: Offspring values

so the new type of the central mother is about to be generated. For each type in the neighbourhood, and for the mother and the mother herself, all offspring are summed up. Table 4 show the offspring values per type in this neighbourhood. The type with the highest offspring value is going to be the type of the mother in the new generation.

The variable  $w$  in the table represents the weight

Type	Summation	Total $w = 1$	Total $w = 2$	Total $w = 3$
Type 1	$2\frac{1}{3} + w * 1\frac{2}{3}$	4	$5\frac{2}{3}$	$7\frac{1}{3}$
Type 2	$2 + 2\frac{1}{3} + 2\frac{1}{3}$	$6\frac{2}{3}$	$6\frac{2}{3}$	$6\frac{2}{3}$
Type 3	$2 + 1\frac{1}{6}$	$3\frac{1}{6}$	$3\frac{1}{6}$	$3\frac{1}{6}$

Table 4: Offspring values per type in neighbourhood

of the central mother. This shows that the type the new generation mother is going to belong to depends on this weight. For  $w < 3$ , the new mother will be an



individual of type 2, but for  $w \geq 3$  the new mother will be an individual of type 1.

## 4 Experiments

The LRD model has three important variables: the fitness matrix, the size of the neighbourhood and the weight of the mother individual during the calculation of the offspring. In this section the focus is on experimenting with variables. Later a case study inspired on biological cells is performed.

To be able to play with these variables there is a standard example.

The original population for this standard example,

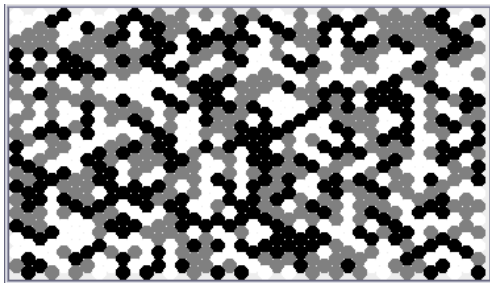


Figure 4: Standard population with 800 individuals (hexagons).

figure 4, consists of 800 individuals that each belong to one of the three types that occur in this population, called *Black*, *Gray* and *White*. The individuals are randomly placed using a pseudo-random generator. Fitness matrix  $A$  from figure 3 is used to create the offspring values, the neighbourhood only includes the direct neighbours and the weight for the mother individual is set to one, so all individuals have equal influence on each other. Figure 5 shows how this population evolves by generating generation after generation.

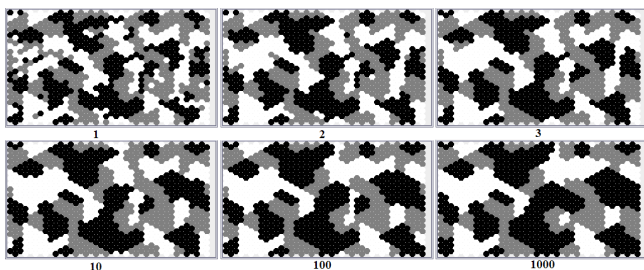


Figure 5: Standard example where the numbers indicate the generations.

### 4.1 Variables

The influence of the variables are clarified by testing the model. The focus lies on the fitness matrix but the weight of the mother and size of the neighbourhood also have influence on how individuals interact with each other.

#### WEIGHT

The influence of the weight of the mother individual is already shown in the example from section 3.3. The composition of the population looks differently for different weight, for the mother, for example setting the weight to zero. The results for the standard population with the standard matrix, standard neighbourhood but weights equal to zero are shown by figure 6.

Comparing these results to the results of the

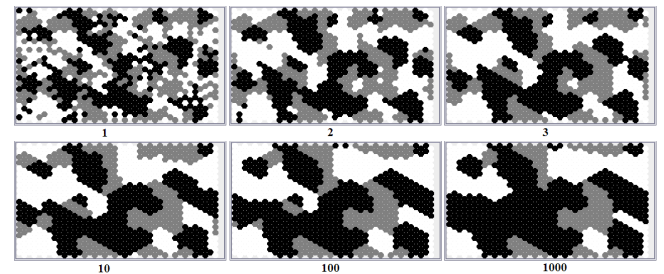


Figure 6: Generations for weight = 0.

standard example the composition is differently but what about the scale of the types in the population? The higher the weight of the mother cell, the faster the population scale stabilizes. But the scale of types differs per weight value anyway. The graphics in figure 7 visualize this observation. The black line indicates the fraction of the *Black* types in the population, the dark gray line indicates the fraction *Gray* types and the light gray line represents the fraction of *White* types.

The explanation for this observation is straight forward. If the values of the mother's weight is sufficiently high, no the mother type will be affected by another type.

#### DISTANCE

The smallest neighbourhood consists only of the direct neighbours. But of course this can be extended. By taking more neighbours into account the composition of the population changes differently. The minorities in the group have less chance to survive once they form a small group. Once a type dominates over fifty percent of the total area, that type takes over if the neighbourhood distance used is high enough. If the distance is as large that the neighbourhood contains all individuals in the population, then the local model gives the same results as the classical global model.

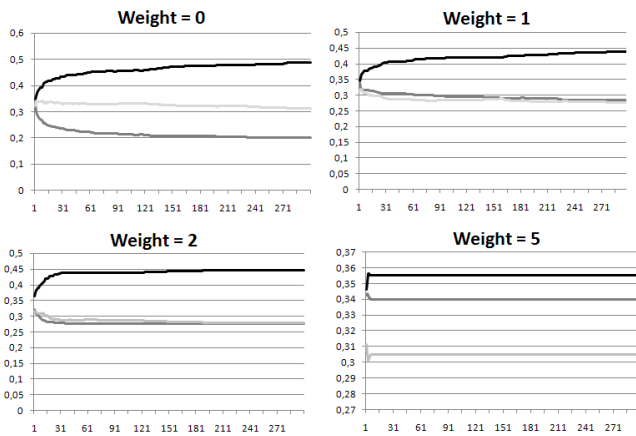


Figure 7: Scale of types for different weights.

FITNESS MATRIX

Generating the new population is highly affected by

$T$	B	G	W	$Q$	B	G	W	$R$	B	L	W	D
Black	1	3	3	Black	1	2	1	Black	3	4	1	3
Gray	2	2	3	Gray	2	3	2	Light Gray	2	4	3	1
White	1	1	2	White	1	2	1	White	4	5	4	2
								Dark Gray	3	1	5	2

Figure 8: Three different matrices with fitness values.

the values from the fitness matrix. The choice of the weight and the neighbourhood distance can increase or decrease the influence of the matrix values. On basis of the three matrices shown in figure 8 the influence of the fitness matrix is explained, with mother weight and neighbourhood distance each set to one.

Matrix  $T$  is a matrix where the gray type is always doing better than the white type. The prediction from the classical model would be that the white types would disappear from this population. But figure 9(a) shows that the white types stay alive though only with a small number of individuals. The explanation is that the white types can survive as long as they have enough individuals of the black types around them. This can be shown by changing the entry  $T(black, black)$  to 2, and call the new matrix  $T^*$ . Figure 9(b) displays the scale graph that belongs to  $T^*$ . Now the white types are died away from the total population since also the black type is always better than the white type.

The second fitness matrix, matrix  $Q$ , has one dominant type, the gray type. The other two types maintain together which means that as long as there are enough individuals of their own type and the other recessive type, they will both survive. The evolution of this population in figure 10 visualizes the recessive

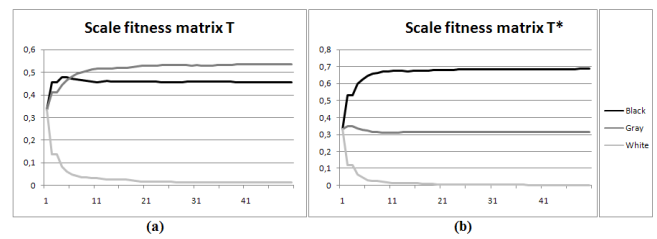


Figure 9: Scales of types for two slightly different matrices.

behaviour of two types according to the dominant types. Matrix  $R$  is a fitness matrix for four different types

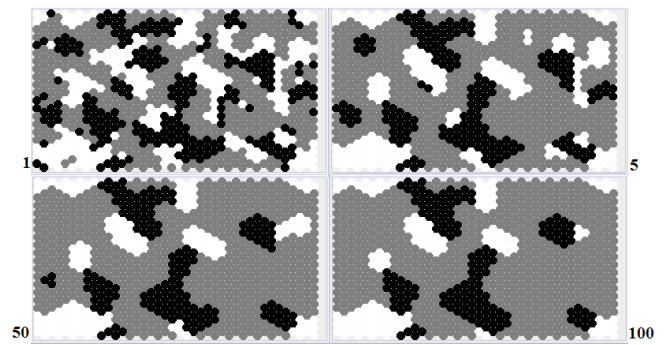


Figure 10: Evolution of dominant vs recessive behaviour (numbers indicate generations).

in the population. For this example a population with 16200 individuals is used, again the mother weights and the neighbourhood distance are set to one. According to the matrix, the white types dominates the light gray types. This would mean that the light gray types would disappear after a long time in the classical model. The evolution of the scale of types in the population is shown by figure 11, but this graph does not imply the extinction of the light gray types.

The graph shows that the white type dominates all

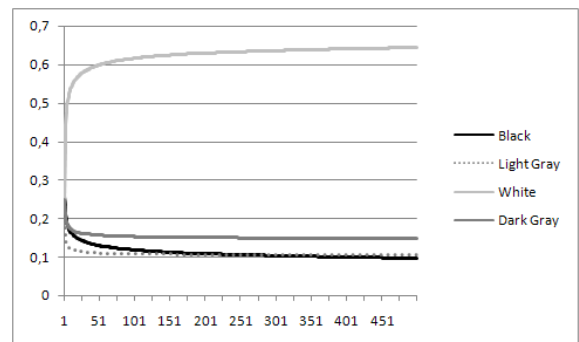


Figure 11: Scales of types for matrix  $R$ .

and that the other three types are recessive. The three



recessive types behave like the two recessive types for matrix  $Q$ , where the black type has even less individuals left than the light gray types which were likely to go extinct. Figure 12 visualizes how the types stick together after 1000 generations, the dominant type is all around those clustered white types.

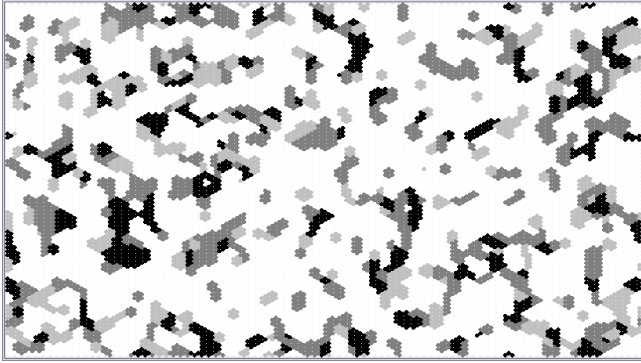


Figure 12: Population composition after 1000 generations for matrix  $R$

OBSERVATIONS

As the images in this section show, applying LRD leads to clustering of individuals that belong to the same types. Using the three variables in the right way it is possible to influence the clustering. Another observation made is the clustering of different types. Recessive types can stay alive by joining each other, while they disappear if they are surrounded by dominant types of individuals. Knowing all the possibilities of all these variables, the reality could be simulated. Next section shows a case study on cell biology, a first attempt in trying to simulate the behaviour of tumor cells among normal cells.

4.2 Case Study

The existence and growth of tumors are well-known problems related to Biology. Biologists have conducted many years of research to this subject. Their findings up to now show that tumor cells do not have the ability to stabilize, while normal cells do. Besides that, not all tumorcells can be destroyed. This depends on the interaction between cells. Apparently most cells in human tissue do not interact with other cells. The ones that do interact, have the connection factor and are able to destroy tumor cells. Since tumor cells used to be normal cells, they have the same interaction skills: some can interact due to the connection factor and some can not. None of the normal cells can destroy a tumor cell that can not interact. Tumor cell that can interact, can be destroyed by a normal cell that is able to interact. The

interaction works actually more complicated, this is only a simplification of the reality for our model.

With this simple background knowledge matrix  $Z$ , figure 13, is formed. Type  $Normal^-$  indicates normal cells that not can interact with other cells, they form a stable tissue. The normal cell that can interact with other cells belongs to type  $Normal^+$ . For the tumor cells are the ones that can interact with other cells of type  $Tumor^+$ , the tumor cells that never get destroyed are of type  $Tumor^-$ .

The stable normal cells get one offspring with all

$Z$	$N^-$	$N^+$	$T^-$	$T^+$
$Normal^-$	1	1	1	1
$Normal^+$	1	1	2	2
$Tumor^-$	2	2	2	2
$Tumor^+$	2	0	2	2

Figure 13: Fitness matrix  $Z$ .

individuals, no matter of what type they are. The tumor cell that does not interact, doubles that amount of offspring because a tumor maintains growing no matter what. The normal cell that can interact grows twice as fast when it meets a tumor cell. It does not matter what kind of tumor cell. The tumor cell that can be destroyed only dies when it comes across a cell of type  $Normal^+$ , otherwise it behaves like the standard tumorcell.

Since the normal cells are stabilized and the tumor cells keep on growing it is likely that the normal cells will die and the tumor cells will survive. Figure 14 visualizes the scales of the types over fifty generations. The number of normal cells that can not interact is greatly reduced. The normal cells with the connection factor are more present, but this can be explained by the fact that they grow when they meet a tumor cell. Since the tumor cells take a large percentage of the population, the connecting normal cells have enough cells around them to grow.

In the evolution of this population the observations in previous section get visible. In figure 15 it is easy to see the clustering. The clustering of normal cells that cannot interact with normal cells that can is the explanation that those clustered cells do not die away. Also remarkable are the clusters of type  $Normal^+$  next to clusters of  $Tumor^+$ . This links to the observation of clustering types. These types keep each other alive while the tumor cells should be able to take over all normal cells. If the distance would be raised, this could happen but since only the direct neighbours are taken into account, this is not the case for now. With more visualizations we see clusters of  $Normal^+$  cells left at places where the other normal cells used to be and were next to those cells. The  $Normal^-$  cells were staying alive



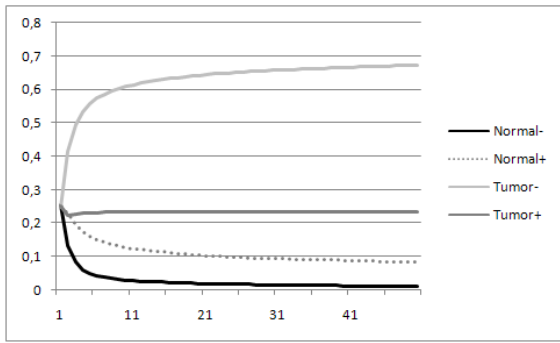


Figure 14: Scales of the different types of cells.

surrounded by  $Normal^+$  cells. But when there came more and more tumor cells around the  $Normal^+$  cells, they started making more offspring. Therefore they reject the stable cells.

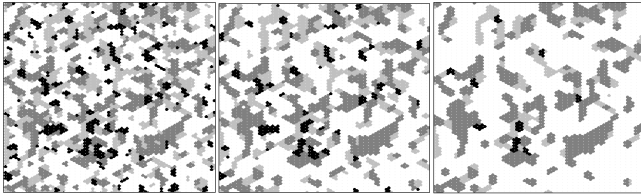


Figure 15: Evolution of tumor and normal cells.

## 5 Global versus Local

Now the idea of the local approach is clear, both models can be compared to each other. The classical model of GRD is set to similar experiments as the LRD<sup>2</sup>. For these experiments several matrices of previous sections are used to compare results immediately.

The evolution of the population using matrix  $A$ , figure 3, stabilizes almost immediately. This can be seen in the left picture of figure 16, which also shows that the beginning is a bit disturbed. The explanation is that also for this approach the starting population is generated by a pseudo-random generator. The local result, the right of the same figure, are not the same, so locally there is some different action than looking globally.

Figure 17 shows the results for matrix  $T$ . The white type should almost die out, according to the local approach. But with the global approach has a bit over 20 percent of the population the color white, the other nearly 80 percent has the other two colours, equally divided. The black line lies behind the gray line, so this is not completely clear from the picture. This again shows

<sup>2</sup>Note that not all graphs, representing the results for these experiments, have the same scales at the axes.

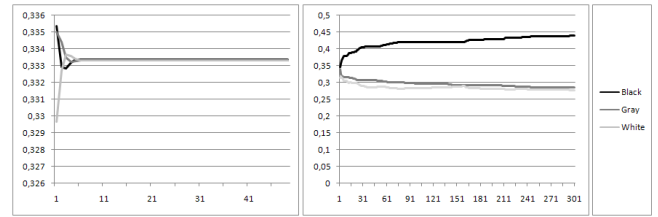


Figure 16: Scaling graphs for matrix  $A$ .

that the local approach has different interaction than the global approach.

For matrix  $R$  the results for the global approach, left

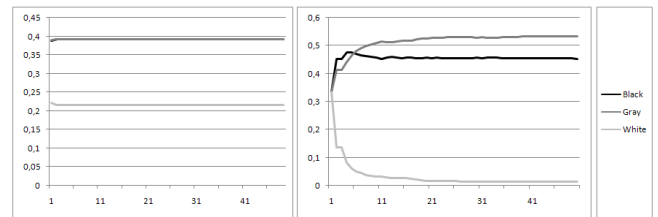


Figure 17: Scaling graphs for matrix  $T$ .

of figure 18, does not seem to be different from the local results, right. But by looking at the vertical axes of both graphs the difference becomes larger. The vertical axis from the local scale graph is twice as large as the axis of the other graph, thus there is a major difference between them. Dominance has more impact at local level than when looking globally, as it seems. But at the end, the population with local interaction has more dominant individuals than the population at a global level.

The final matrix to be discussed is the matrix from

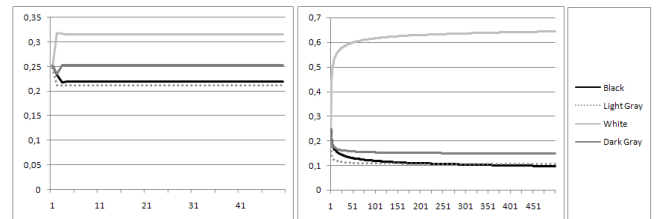


Figure 18: Scaling graphs for matrix  $R$ .

the case study. The previous section explained the idea behind the matrix and the results from local behaviour seemed quite straightforward. But how does the population with matrix  $Z$  evolve according to the global approach? The left picture in figure 19 shows a quite different scaling of the types in the population than the right picture. Those results are from the global approach, the negative normal cells would not die out, they stabilize and have a little over 15 percent of the population. The other normal type has 25 percent of the population, so





60 percent of all cells are tumor cells. This percentage is way less than the percentage at local level interactions in the population. At local level the tumor cells take about 90 percent of the population.

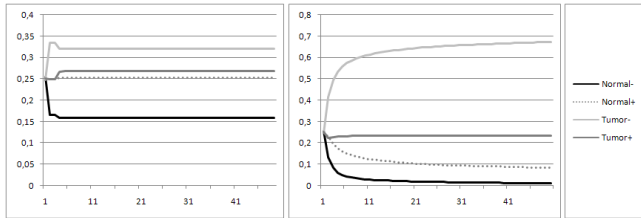


Figure 19: Scaling graphs for matrix  $Z$ .

## 6 Conclusions

The focus of this paper was on local interactions between individuals in an evolutionary game setting. The main question in this paper was "How does a population evolve when applying LRD compared to GRD?"

Experiments showed that the population does not stay equally divided as in the GRD approach but all types cluster together. This can lead to clusters per type but also clusters of different types together. Clustering gives minorities the probability to survive instead of dying out.

In the case study the LRD showed the predicted behaviour, but the GRD showed a completely different view. This shows that the LRD is more capable to simulate future generations than GRD.

Modelling the interaction of individuals is needed to predict the future. Some parts in this model that could be generalized upon are the weights, the influence of distance, the inclusion of possible mutations and a different approach for deriving the numbers of offspring.

The weights of different types could vary. This means that not all types have the same influence for creating own offspring. In case of the case study, the tumor cells could have weight two and normal cells have weight one. So tumor cells grow twice as fast as the normal cells. The fitness matrix could be changed, with mostly ones in it. Only the zero value and the value two for the normal cells remain. This could lead to the same results, but that should be studied more closely.

The influence of neighbours, that are not directly adjacent to the mother individual, could be less. Since they are further away it is likely that they have less influence on the mother. Therefore one could assign weights to all neighbour individuals in the neighbourhood based on their distance to the mother.

Variance in a population is often caused by mu-

tations. The occurrence of mutations is a natural phenomenon. Including this in the model and creating a way so that the model can incorporate these, would be a big improvement.

The approach for deriving the number of offspring in this LRD model is by expectations. Instead, the mother could choose a partner from the assigned neighbourhood randomly, and would get the number of offspring as the value of entry (mother, father) from the fitness matrix indicates. So, instead of working with expectations, we could also work with the realizations of all these probabilistic events.

It is not clear whether or not the two models would give highly similar results. So further studies are needed.

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