Modeling, Simulation and Application of Bacterial Transduction in Genetic Algorithms

Carlos Perales-Graván

Department of Applied Mathematics, Faculty of Biological Sciences

Complutense University of Madrid, Madrid 28040, Spain

Javier de Vicente Buendia

Department of Applied Mathematics and Statistics,

E.T.S.I. Aeronautics Polytechnic University of Madrid, Madrid 28040, Spain

Rafael Lahoz-Beltra (1)

Department of Applied Mathematics, Faculty of Biological Sciences

Complutense University of Madrid, Madrid 28040, Spain

(1) Corresponding author. Tel.: +34-91-3944888, FAX: +34-91-3945051

E-mail: lahozraf@bio.ucm.es

Abstract

At present, all methods in Evolutionary Computation are *bioinspired* in the fundamental principles of neo-Darwinism as well as on a vertical gene transfer. Thus, on a mechanism in which an organism receives genetic material from its ancestor. Horizontal, lateral or cross-population gene transfer is any process in which an organism transfers a genetic segment to another one that is not its offspring. Virus transduction is one of the key mechanisms of horizontal gene propagation in microorganism (e.g. bacteria). In the present paper, we model and simulate a transduction operator, exploring a possible role and usefulness of transduction in a genetic algorithm. The genetic algorithm including transduction has been named PETRI (abbreviation of *Promoting Evolution Through Reiterated Infection*). The efficiency and performance of this algorithm was evaluated using a benchmark function and the 0/1 knapsack problem. The utility was illustrated designing an AM radio receiver, optimizing the main features of the electronic components of the AM radio circuit as well as those of the radio enclosure. Our results shown how PETRI approaches to higher fitness values as transduction probability comes near to 100%. The conclusion is that transduction improves the performance of a genetic algorithm, assuming a population divided among several sub-populations or 'bacterial colonies'.

Keywords

Bacterial genetic algorithm, horizontal gene transfer, conjugation operator, transduction operator.

1. Introduction

At present, all methods in Evolutionary Computation (genetic algorithms, evolutive algorithms, genetic programming, etc.) are *bioinspired* in the fundamental principles of neo-Darwinism (Lahoz-Beltra, 2008) as well as on a vertical gene transfer. That is, on a mechanism in which an organism receives genetic material from its ancestor from which it evolved. In fact, most thinking in Evolutionary Computation is focused on vertical gene transfer as well as in crossover and/or mutation operations.

Microorganisms have been evolving on Earth for billions of years. Nowadays, there are several reasons for which microbial evolution experiments have received increasing attention (Elena and Lenski, 2003). Such experiments include many bacteria and viruses as well as unicellular fungi. Microbiologists known from many years ago how bacteria are able to adapt and evolve in all kinds of environments. Bacteria are microscopic organisms whose single cells reproduce by a process of binary fission or asexual reproduction bearing a resemblance with John von Neumann's universal constructor (1966). Thus, a bacterium is a self-replicating machine which chromosome is replicated and a copy is allocated to each of the bacterium daughter cells. Both daughter cells are identical excepting for those mutations occuring in daughter cells. A bacterial population (or colony) evolve according to an evolutive algorithm similar to Dawkin's biomorphs (Dawkins, 1986), powering their evolution the cumulative selection of mutations. For a long time, bacteria were thought to lack sexual reproduction and in consequence a way to transfer genetic material between cells. However, bacteria as single-cell organisms exhibit significant phenomena of genetic transfer and crossover between cells. This kind of mechanisms belong to a particular kind of genetic transfer known as horizontal gene transfer. Horizontal, lateral or cross-population gene transfer is any process in which an organism, i.e. a donor bacterium, transfers a genetic segment to another one, a recipient bacterium, which is not its offspring. In the biological realm, whereas the scope of

vertical gene transfer is the population, in horizontal gene transfer the scope is the biosphere. This particular mode of *parasexuality* between 'relative bacteria' includes three genetic mechanisms: conjugation, transduction and transformation. In a previous paper (Perales-Graván and Lahoz-Beltra, 2008) we introduced an evolutionary algorithm through the substitution of crossover operation in a genetic algorithm by conjugation. Furthermore, microorganisms are very interesting individuals because they also exhibit 'social interactions'. Recently we found (Lahoz-Beltra et al., 2009) how the inclusion of the 'social life of microorganisms' into the genetic algorithm cycle, significantly improves the algorithm's performance.

In Nature, microorganisms such as bacteria and viruses share a long and common evolutive relationship. This relationship is mainly promoted by bacteriophages (or phages) (Davis et al., 1990), thus a kind of viruses that multiply themselves inside bacteria by making use of the bacterial biosynthetic machinery. Some bacteriophages are able to move bacterial DNA (the 'bacterial chromosome') from one bacterium to another. This process is known as transduction. When bacteriophages infect a bacterial cell, their normal mode of reproduction uses the replication machinery of the bacterium, making numerous copies of its own viral genetic material (i.e. DNA or RNA). Soon the nucleic acid copies (or chromosome segments) are then packaged into newly synthesized copies of bacteriophage virions. Considering the life cycle of a particular bacteriophage, we can define two sorts of transduction (Figure 1). Generalized transduction occurs when 'any part' of the bacterial chromosome (instead of viral DNA) hitchhikes into the virus (i.e. T4 phages in *Escherichia coli* bacterium). However, when only 'specific genes' or certain special 'segments' of the bacterial chromosome can be transduced, such mistake is named as specialized transduction (i.e. phages in *Escherichia coli* bacterium). Here we study the possibility of developing genetic algorithms including transduction operations as horizontal gene transfer mechanism. The efficiency and performance of transduction was evaluated using a benchmark function and the 0/1 knapsack problem. The utility was

illustrated designing an AM radio receiver, optimizing the main features of the electronic components of the AM radio circuit as well as those of the radio enclosure. Our results show how transduction improves the performance of a genetic algorithm, assuming a population divided among several sub-populations or 'bacterial colonies'.

It is important to point out that even when transduction in real bacteria involves migration at 'cellular level' and subsequent crossover, it is not the simple addition of both mechanisms. That is, Figure 2 depicts transduction operations as they are simulated in the present paper. To show differences between transduction (Figure 2a-b) and migration-crossover, Figure 2c illustrates how migration and crossover events must occur in bacterial cells. In consequence, in transduction the transference of chromosome segments (Figure 2a) between bacterial populations or colonies is very different of migration (the occasional exchange of individuals). Migration and transduction could bear a resemblance, but only when transduction involves the complete chromosome transference (Figure 2b) between bacterial populations. Furthermore, this kind of transference is a highly unlikely event in bacteria, taking place in these microorganisms the transduction of chromosome segments as is shown in Figure 2a.

In this paper, we model and simulate the two kind of transduction operations described above (Figure 2a-b), examining a possible role and usefulness of this genetic mechanism in genetic algorithms. In a previous paper (Perales-Gravan and Lahoz-Beltra, 2008) we introduced a bacterial conjugation operator (Figure 3), showing its utility designing an AM radio receiver (Figure 4). Conjugation is one of the key genetic mechanisms of horizontal gene transfer between bacteria. Now, in the present paper we refer to a genetic algorithm including transduction as PETRI (abbreviation of *Promoting Evolution Through Reiterated Infection*). We have investigated the transfer of genes and chromosomes among sub-populations with a simulated 'bacteriophage'. In the model we consider a structured population divided among several sub-populations or 'bacterial

colonies', bearing a resemblance with coarse grained distributed genetic algorithms. Each sub-population is represented as a Petri dish (a glass or plastic cylindrical dish used to culture microorganisms). However, note that even when we divide a population into sub-populations the proposed algorithm is sequential. Thus, the algorithm is not a distributed one since we used a mono-processor computer and the algorithm has not been parallelized. Moreover, the migration mechanism is synchronous since genes and chromosome transferences were both between sub-populations and during the same generation. Therefore, our approach could be related with those models of Cellular Genetic Algorithms (cGA) (Alba and Dorronsoro, 2008) adopted also for mono-processor machines, with no relation to parallelism at all. Nevertheless, the cGA concept of neighborhood is replaced by the notion of sub-population or 'bacterial colony' and the migration of solutions is substituted in our approach by the mechanism of transduction. In our model we assumed that bacteria are able to display crossover through conjugation instead performing one-point or two-points recombination. Moreover, we assume that no vertical gene transfer mechanism is present in bacterial populations.

With the purpose to study the performance of the transduction operator, we used different optimization problems. Experiments carried out in presence of transduction were compared with control experiments, thus experiments performed in absence of transduction. Similarly, we compared the transduction performance under the three types of crossover: conjugation, one-point or two-points recombination. We are interested in the study of genetic algorithms based on horizontal gene transfer mechanisms, mainly conjugation and transduction operations. It is important to note that even when conjugation and transduction are both horizontal gene transfer mechanisms, there are some relevant differences between both. In first place, whereas conjugation involves two bacteria from the same population, the bacteria involved in transduction could belong to different populations. In consequence, conjugation is a genetic mechanism of horizontal gene transfer *within* a population, whereas transduction is a genetic mechanism of

horizontal gene transfer *between* populations (Figure 5). Secondly, in conjugation the length of the transferred genetic segment is variable, whereas in transduction the transferred segment length is always constant. In Section 2 of this paper, we present the model description and PETRI algorithm, and in Section 3 we describe several simulation experiments. Section 4 introduces the statistical analysis, and Section 5 presents the whole results of the computer simulation experiments. Finally, Section 6 discusses the possible impact of this work, suggesting future directions of advancement.

2. Model description

In this section, we introduce the transduction model as well as the PETRI implementation, thus the algorithm that results once transduction is included into a genetic algorithm.

2.1. Transduction model

Let b be a chromosome (i.e. bacterium; 1,.., j ,..., N) and p a sub-population (i.e. Petri dish; 1 ,..., i ,..., P) then a transduction operation (Figure 2) is defined as follows. Transduction is the transfer of genetic material from a Petri dish and bacterium donors (p^D, b^D) to a Petri dish and bacterium recipients (p^R, b^R). When the transference involves a chromosome segment (Figure 2a) the result is a recombinant chromosome in the recipient Petri dish p^R. However, the transference of a complete chromosome (Figure 2b) results in the substitution of one chromosome of the recipient Petri dish p^R by the transferred one. It is important to note that 'bacterium' and 'Petri dish' terms are used along the paper as 'chromosome' and 'sub-population' synonyms, respectively.

The donors, Petri dish and bacterium, are both selected applying one of the following criteria. Let p^D be the donor Petri dish representing the sub-population from which to select the donor bacterium. The selection of the donor Petri dish is based on one of the following criteria:

a) Random selection (method *r*).- In this case a Petri dish p^D is chosen at random from a uniform distribution according with the range [1, *P*].

b) Maximum fitness (method *max*).- Given *P* Petri dishes, the Petri dish p^D with maximum fitness is selected. Thus, if $\overline{f_i}$ is the fitness value of the *i*th donor Petri dish, then we select $\max_{1,\ldots,P}\left\{\overline{f_1}, \overline{f_2}, \ldots, \overline{f_i}\right\}$.

c) Average fitness (method *ave*).- Given *P* Petri dishes, the most representative Petri dish p^D with fitness value $\overline{f_i}$ is selected, such that $\min_{1,\ldots,P}\left|\overline{f_i} - \overline{f_p}\right| \geq 0$ where $\overline{f_p}$ is the average fitness of the *P* donor dishes.

d) Roulette wheel dish selection (method *roul*).- In this case a Petri dish p^D is chosen spinning a roulette wheel that assigns to each dish a slot whose arc size is proportional to its fitness value $\overline{f_i}$.

Once a donor Petri dish is selected, the choice of the donor bacterium b^D is conducted according to one of the following criteria:

a) Random selection (method *r*).- In this case a bacterium b^D is chosen at random from a uniform distribution according with the range [1, *N*].

b) Maximum fitness (method *max*).- Given N bacteria, the bacterium b^D with maximum fitness is selected. That is, such that $\max_{1,..,N}\{ f_1 , f_2 ,..., f_j\}$ where f_j is the fitness value of the jth donor bacterium.

c) Average fitness (method *ave*).- Given N bacteria, the most representative bacterium b^D with fitness value f_j is selected, such that $\min_{1,..,N}\left| f_j - \overline{f} \right| \geq 0$ where $\overline{f}$ is the average fitness of the bacterial population or donor Petri dish p^D.

d) Roulette wheel bacterial selection (method *roul*).- In this case a bacterium b^D is chosen spinning a roulette wheel that assigns to each dish a slot whose arc size is proportional to its fitness value f_j. Note that this method is the well-known roulette wheel parents selection.

The recipient Petri dish and bacterium are both selected as follows. The selection of the recipient Petri dish p^R is conducted through one of the following criteria:

a) Random selection (method *r*).- In this case a Petri dish p^R is chosen at random from a uniform distribution according with the range [1, P].

b) Minimum fitness (method *min*).- Given P Petri dishes, the Petri dish p^R with minimum fitness is selected. That is, $\min_{1,..,P}\{ \overline{f_1}, \overline{f_2},..., \overline{f_i}\}$ where $\overline{f_i}$ is the fitness value of the ith recipient bacterium.

c) Average fitness (method *ave*).- Given P Petri dishes, the most representative Petri dish p^R with fitness value $\overline{f_i}$ is selected. Thus, $\min_{1,..,P}\left| \overline{f_i} - \overline{f_p} \right| \geq 0$ where $\overline{f_p}$ is the average fitness of the P recipient dishes.

d) Inverse roulette wheel dish selection (method *inv roul*).- In this case a Petri dish p^R is chosen spinning a roulette wheel that assigns to each dish a slot whose arc size is proportional to the inverse of its fitness value, thus $1/f_i$.

Once a recipient Petri dish is chosen, the selection of the receptor bacterium b^R is conducted according to one of the following criteria:

a) Random selection (method *r*).- In this case a bacterium b^R is chosen at random from a uniform distribution according with the range [1, *N*].

b) Minimum fitness (method *min*).- Given *N* bacteria, the bacterium b^R with minimum fitness is selected. That is, $\min_{1,..,N}\{ f_1 , f_2 ,..., f_j\}$ where f_j is the fitness value of the *j*th recipient bacterium.

c) Average fitness (method *ave*).- Given *N* bacteria, the most representative bacterium b^R with fitness value f_j is selected, such that $\min_{1,..,N}\left| f_j - \overline{f} \right| \geq 0$ where $\overline{f}$ is the average fitness of the bacterial population or recipient Petri dish p^R.

d) Inverse roulette wheel bacterial selection (method *inv roul*).- In this case a bacterium b^R is chosen spinning a roulette wheel that assigns to each dish a slot whose arc size is proportional to the inverse of its fitness value, thus $1/f_j$.

2.2. PETRI: A genetic algorithm with simulated transduction.

The current PETRI (abbreviation of *Promoting Evolution Through Reiterated Infection*) algorithm (Figure 6) uses a population size of N, performing r_e replicates, with P being the total number of Petri dishes or sub-populations. Thus, we performed a number of $r_e.P$ trials of each simulation experiment. The algorithm cycles through epochs (Figure 7) searching for an optimum solution until a maximum of G generations is reached. Once (p^D, b^D) and (p^R, b^R) are selected, only one 'bacteriophage' is assumed to participate during each transduction event. The PETRI algorithm is summarized in the following pseudocode description:

```
/* PETRI: Genetic Algorithm with Transduction */
1. t:=0;
2. Initialization: Generate P Petri dishes (or sub-populations)
   with N random bacteria (or chromosomes).
3. WHILE not stop condition DO
      /* Genetic Algorithm */
       (3.1) FOR each P Petri dish DO
             Evaluation of chromosomes
             Selection
             Crossover (conjugation, one-point, two-points)
             Mutation
       (3.2) END FOR
     /* End of Genetic Algorithm */
4. Transduction: (pᴰ, bᴰ)  (pᴿ, bᴿ)
5. t:=t+1;
6. END WHILE;
/* End of PETRI */
```

Starting with a random population of chromosomes (or bacteria) selection, crossover, mutation, and transduction were simulated, obtaining new generations of equal population size. Once the initial population of chromosomes was obtained at random, the order in which the genetic operators were applied was in agreement with the protocol

SDS (Lahoz-Beltra, 2001; Perales-Gravan and Lahoz-Beltra, 2004). This protocol is inspired in DNA shuffling, an experimental method used in biotechnology for improving *in vitro* protein activity and functionality. In the present simulation experiments, the protocol SDS (Figure 8) involves a cycle of crossover and mutation, as well as transduction, through n_g generations. This phase is followed by repeated cycles of crossover and transduction, one per generation, in absence of mutation. Considering the performance of experiments previously conducted the simulation experiments were carried out setting up n_g equal to 25.

2.2.1. Selection

At each generation, the fitness of each chromosome was evaluated using a fitness function that depends on the chosen optimization problem. Once the chromosomes are evaluated, we selected the crossover (or mating) pool of the next generation using the roulette wheel parents selection algorithm (Goldberg, 1989; Lahoz-Beltra, 2004). Of course, other selection schemes are possible such as tournament selection, truncation selection, as well as linear and exponential ranking selection. However, the roulette wheel parents selection scheme bears a better resemblance to Darwinian natural selection (Lahoz-Beltra, 2001).

2.2.2. Crossover

Once a new generation of offspring chromosomes is obtained, then pairs of chromosomes are randomly selected *within* a sub-population or Petri dish. Once a couple of chromosomes (or bacteria) {#*i*, #*j*} is selected, whether or not we are going to perform crossover on the current pair of chromosomes {#*i*, #*j*} is decided on the basis of a Bernoulli trial regarding conjugation as having a given probability p_c (or alternatively instead conjugation, crossover is conducted via one-point or two-points recombination).

2.2.3. Mutation

Mutation of a gene was simulated changing at random the value gene, choosing the mutated value from a uniform distribution with similar range of those defined to obtain the initial population of chromosomes. Once again, whether or not to change a gene value on a chromosome is decided on the basis of a Bernoulli trial, mutation being a success with a given probability p_m (mutation probability).

2.2.4. Transduction

Transduction was simulated based on the model described in Section 2.1. The operator requires the selection of the Petri dish and bacterium donors (p^D, b^D) as well as the Petri dish and bacterium recipients (p^R, b^R). Once (p^D, b^D) and (p^R, b^R) are both selected, whether or not we are going to perform transduction on the current pair is decided on the basis of a Bernoulli trial regarding transduction as having a given probability p_t (transduction probability).

3. Simulation experiments

The performance of the simulated transduction was studied considering three optimization problems. The first problem uses a benchmark function and the second one is the 0/1 knapsack problem. Finally, we illustrated the usefulness of the transduction in a real-life application problem described in Perales-Gravan and Lahoz-Beltra (2008).

3.1. Experiment 1

A first optimization problem was an instance of the Michalewicz function. We used 10 variables or genes, such that:

$$f(x) = \sum_{i=1}^{10} sen(x_i) \cdot sen\left(\frac{i \cdot x_i^2}{\pi}\right)^{2m}; \qquad 0 \leq x_i \leq \pi \qquad (1)$$

The simulation experiments were carried out with N = 500 chromosomes (or bacteria), r_e = 15 and P = 4 Petri dishes. Therefore, we performed 60 trials (15 replicates x 4 Petri dishes) of each experiment. The transduction experiments were conducted transferring only complete chromosomes, cycling the algorithm through epochs searching for an optimum until a maximum of 700 generations (G) is reached. In each trial, we calculated the population average fitness at the last generation. The crossover and mutation probabilities were set up to p_c=0.75 and p_m=0.05, respectively. When crossover was simulated through conjugation then the conjugation parameter was set up as $\alpha = 0.5$.

Since preliminary results (*experiment 3*) suggested which one is the best transduction policy, transduction was simulated selecting donors (p^D, b^D) based on *max-max* criterion, and recipients (p^R, b^R) using *roul-r* criterion. The simulation experiments were conducted setting up the transduction probabilities p_t to 0% (control experiment, without transduction), 25%, 50%, 75% and 100%. We performed simulation experiments with PETRI using conjugation, one-point recombination and two-points recombination.

3.2. Experiment 2

A second optimization problem was the well-known 0/1 knapsack problem. Assume we have j kinds of items and each item has a value v_j and weight w_j, being the maximum weight that we can carry in the knapsack equal to W. The 0/1 knapsack

problem restricts the number of each kind of item x_j to 0 or 1. The aim is to maximize $\sum_j v_j x_j$ subjected to $\sum_j w_j x_j \le W$. The fitness was calculated by the usual expression:

$$f(x) = \begin{cases} \sum_j w_j x_j \quad W, \sum_j v_j x_j \\ \sum_j w_j x_j > W, W - \sum_j w_j x_j \end{cases} \quad (2)$$

using the benchmark knapsack instance 'knap100' published on a web site by the Swiss Federal Institute of Technology Zurich (2008). The instance includes the values and weights of 100 items being maximum weight W=2732. The simulation experiments were carried out with N = 200 chromosomes (or bacteria), r_e = 15 and P = 4 Petri dishes, conducting 60 trials (15 replicates x 4 Petri dishes) of each experiment. The transduction experiments transferred only complete chromosomes, cycling the algorithm through epochs until a maximum of 1000 generations (G) is reached. In each trial, we obtained the maximum fitness at the last generation. The crossover and mutation probabilities were set up to p_c=0.75 and p_m=0.05, respectively. When crossover was simulated through conjugation then the conjugation parameter was set up as $\alpha = 0.5$. Once again, transduction was simulated selecting donors (p^D, b^D) based on *max-max* criterion and recipients (p^R, b^R) using *roul-r* criterion. The transduction probability p_t was set up to 0% (control experiment, without transduction), 25%, 50%, 75% and 100%. We performed simulation experiments with PETRI using conjugation, one-point recombination and two-points recombination.

3.3. Experiment 3

An example of the usefulness of transduction in a real-life application problem consists in finding the main features of the electronic components of an AM radio

receiver as well as those of the radio enclosure. The current PETRI algorithm uses a population size of 500 (N) and 9 (P) Petri dishes, performing fifty replicates (r_e). Therefore, we performed 450 trials (50 replicates x 9 Petri dishes) of each experiment. The algorithm cycles through epochs searching for an optimum AM radio receiver until a maximum of 200 generations (G) is reached. In each trial, we calculated the population average fitness at the last generation. The crossover and mutation probabilities were set to p_c=0.75 and p_m=0.05, respectively. Since crossover was simulated via conjugation, the parameter α was set to 0.5. The initial population of chromosomes (Figure 3) was obtained at random, choosing the gene values from a uniform distribution according with the ranges described in Perales-Gravan and Lahoz-Beltra (2008). At each generation, the fitness of each chromosome, thus the degree of achievement of the AM radio receiver circuit as well as the main features of the radio enclosure, was evaluated using the following fitness function:

$$f = f_{oscillator} \cdot e^{P_D + P_{RC}} + f_{radio\ enclosure} \qquad (3)$$

where $f_{oscillator}$ is the fitness of the oscillator circuit and $f_{radio\ enclosure}$ the fitness of the radio enclosure designed to house the radio circuit. In function (3) P_D as well as P_{RC} are two punishment terms related with diode and RC filter performance, respectively. Considering the intricacy of f, we suggest that for a detailed explanation see Perales-Gravan and Lahoz-Beltra (2008).

3.3.1. Transduction policy

Based on the present optimization problem two types of transduction experiments were conducted depending on that is transferred: chromosome segments (Figure 2a), or a complete chromosome (Figure 2b).

In those experiments with chromosome segments, we studied which one of the criteria described in Section 2.1 leads to a superior conjugation performance. We assume that conjugation results obtained with the AM radio receiver problem could be extended to one-point or two-points recombination crossovers as well as to other optimization problems. In order to simplify the number of possible simulation experiments we assumed that most of the experiments are conducted considering the following restriction: the Petri dish and bacterium donors were both selected applying the same method. Thus, the Petri dish and bacterium donors were both obtained applying random selection, maximum fitness, average fitness and roulette wheel selection. The aforementioned criteria were labeled as *r-r*, *max-max*, *ave-ave* and *roul-roul*, respectively. Similarly, we considered that the Petri dish and bacterium recipients were both selected also applying similar methods, thus: random selection, minimum fitness, average fitness and the inverse roulette wheel selection. The methods mentioned previously were labeled as *r-r*, *min-min*, *ave-ave* and *inv roul-inv roul*, respectively. We also considered for a few cases the possibility that a Petri dish and bacterium were both selected applying different methods. Once the donors (p^D, b^D) and recipients (p^R, b^R) were selected then the chromosome segment to be transduced was chosen at random applying the following method. The genetic segment transferred from b^D to b^R via a simulated bacteriophage (Figure 9) was chosen with a random value s from a uniform distribution with range [0, 2], such that:

$$s = \begin{matrix} 0, & \text{'Oscillator'} \\ 1, & \text{'Diode + RC Filter'} \\ 2, & \text{'Enclosure'} \end{matrix} \quad (4)$$

Note how in this simulation experiment we simulate ‘specialized transduction’, transferring ‘complete blocks’ or chromosome segments. The following transduction simulation experiments were conducted:

a) Donor Petri dish and bacterium (p^D, b^D) are both selected based on *max-max* criterion. The recipients (p^R, b^R) are selected as follows: *roul-roul*, *roul-r*, *roul-min*, *roul-ave*, *roul-max*, *roul-inv roul*, *max-roul*, *max-r*, *max-min*, *max-ave*, *max-max* and *max-inv roul*.

b) Donor Petri dish and bacterium (p^D, b^D) are both selected based on *roul-roul* criterion. The recipients (p^R, b^R) are selected as follows: *roul-roul*, *r-r*, *min-min*, *ave-ave*, *max-max* and *inv roul-inv roul*.

c) Donor Petri dish and bacterium (p^D, b^D) are both selected based on *r-r* criterion. The recipients (p^R, b^R) are selected as follows: *roul-roul*, *r-r*.

d) Donor Petri dish and bacterium (p^D, b^D) are both selected based on *min-min* criterion. The recipients (p^R, b^R) are selected as follows: *roul-roul*, *min-min.*

e) Donor Petri dish and bacterium (p^D, b^D) are both selected based on *ave-ave* criterion. The recipients (p^R, b^R) are selected as follows: *roul-roul*, *ave-ave*.

f) Donor Petri dish and bacterium (p^D, b^D) are both selected based on *inv roul-inv roul* criterion. The recipients (p^R, b^R) are selected as follows: *roul-roul*, *inv roul-inv roul*.

Finally, the transduction experiments with a complete chromosome were only carried out based on the criterion that leads to a better conjugation performance. In view of the obtained results, experiments were performed selecting the donor Petri dish and bacterium (p^D, b^D) with *max-max* criterion, whereas the recipients (p^R, b^R) were selected based on *roul-r* criterion.

4. Statistical analysis

The simulation experiments performance was evaluated as follows. In first place, we obtained the average fitness of each Petri dish at the last generation *G*. Considering that *P* is the total number of Petri dishes and r_e the number of experimental replicates, then the total number of simulation trials was equal to $P.\ r_e$. Following, a Multiple Box-and-Whisker Plot (Tukey, 1977) was obtained with the average fitness values, considering that each plot represents an experimental protocol with $P.\ r_e$ values. Note that we used a Notched Box-and-Whisker Plot. In this plot, a confidence interval for the median is provided by a notch surrounding the median. The endpoints of the notches are located at the median $\pm 1.5\frac{IQR}{\sqrt{n}}$ such that the medians of two boxplots are significantly different at approximately the 0.05 level if the corresponding notches do not overlap. In each experimental protocol, the Notched Box-and-Whisker Plot shows with a cross the mean of the average fitness values (MAF_T) for the $P.\ r_e$ Petri dishes of an experiment. The MAF_T value is given by the expression:

$$MAF_T = \frac{\sum_{k=1}^{P.r_e} \overline{f_k}}{P.r_e} \quad (5)$$

Next, we performed a Kruskal-Wallis test evaluating the assumption that the medians of the average fitness values obtained under different protocols are equal. Note that experimental efficiency increases as the mean of the average fitness values (MAF) increases, thus when the MAF value displaces more to the top inside the box. The box represents the interquartile range of the average fitness values in the Box-and-Whisker Plot. Furthermore, since the length of the box representing the interquartile range is a

measure of variability, given two experimental protocols, that protocol whose box has the longest length will be the protocol driving the population to reach a higher number of optimum solutions (Perales-Gravan and Lahoz-Beltra, 2008).

Only in *experiment 3* we calculated the mean of the average fitness values but now taking into account the Petri dish class. Thus, we obtained MAF values for the donor Petri dishes (MAF_D), the recipient Petri dishes (MAF_R) and for those neither donor nor recipient dishes ($MAF_{\overline{D}\,\overline{R}}$):

$$MAF_D = \frac{\overline{f_D}}{D} \quad (6)$$

$$MAF_R = \frac{\overline{f_R}}{R} \quad (7)$$

$$MAF_{\overline{D}\,\overline{R}} = \frac{\overline{f_k}}{T-D-R} \quad (8)$$

where D is the number of donor Petri dishes and R the number of recipient Petri dishes.

Note that in all the optimization problems (Section 3) D=R, being D and R equal to 1. Therefore, we selected only one donor and recipient Petri dishes per generation.

5. Results

A remarkable result showing the role of transduction was obtained with Michalewicz function. Figure 10 shows how PETRI approaches to the maximum function value (9.66 in our experiments) as transduction probability p_t comes near to 100%. A Kruskal-Wallis test shown with a *p*-value equal to zero, that the differences among

medians were statistically significant at the 95.0% confidence level. Thus, the genetic algorithm performance is significantly improved no matter which one is the crossover operator (conjugation, one-point recombination or two-points recombination). In particular, in absence of transduction the medians of conjugation, one-point recombination and two-points recombination were 8.87, 8.96 and 8.97, respectively. However, when optimization experiments were performed including a transduction operator (transferring a complete chromosome) then the medians of conjugation, one-point recombination and two-points recombination were 9.29, 9.33 and 9.36, respectively. The Bartlett, Cochran, and Levene tests were accomplished, testing the homogeneity of variances. The obtained *p*-values were zero showing that differences among variances are statistically significant at the 95.0% confidence level. The conclusion is that variance (or population variability) depends on transduction. In fact, the population variability reaches a minimum value when a complete chromosome is transferred and the transduction probability p_t equal to 100%. However, it is important to note that in Nature only tiny fragments or chromosomal segments of bacterial DNA are transduced and not coomplete chromosomes. In agreement with Davis and Weller (1998) the genetic material carried by bacteriophages is, conveniently, around 2% the length of the bacterial chromosome. An interesting observation is that even when transduction is a major driving force behind diversity in natural populations, in our simulation experiments transduction bring down the variability of the population. The explanation could be that in natural populations transduction occurs at random and at very low frequencies from 10^{-2} to 10^{-10} (Ogunseitan, 2008), whereas in the conducted experiments the chromosome or its segments were selected with a medium or high probability and based on *max-max* criterion.

The Figure 11 shows a Multiple-Box-and-Whisker Plot of the maximum fitness values obtained in the 0/1 knapsack problem. It is interesting to note how PETRI approaches to highest fitness values as transduction probability p_t comes near to 100%. A Kruskal-Wallis test shown with a *p*-value equal to zero, that the differences among

medians were statistically significant at the 95.0% confidence level. In consequence, algorithm performance is significantly improved no matter which one is the used crossover operator (conjugation, one-point recombination or two-points recombination). In absence of transduction the median value of the obtained knapsacks under conjugation, one-point recombination and two-points recombination were 2601.5, 2639.5 and 2612.0 respectively. However, in presence of transduction with a p_t equal to 100% (transferring a complete chromosome) the median values of the optimized knapsacks were 3214.0, 3253.0 and 3126.0, respectively. The Bartlett, Cochran, and Levene tests were accomplished to examine the homogeneity of variances. The obtained *p*-values were zero showing that differences of variances between the set of experiments without transduction (labeled as 1, 6 and 11 in Figure 11) and the experiments including transduction are statistically significant at the 95.0% confidence level. Once again, we conclude that variance depends on transduction, decreasing the population variability when a complete chromosome is transferred.

Based on above results we achieved the following general conclusion. Transduction helps the population to reach a better optimum solution and it has an effect on population variability. However, the optimum that is achieved with the transduction of chromosome segments is always below with respect to the optimum that is reached when transduction transfers a complete chromosome. On the other hand, when transduction involves chromosome segments the population variability (or variance) is greater than the variability that results of a complete chromosome transduction. That is, in agreement with Figure 13, transduction of complete chromosomes, a mechanism that bears a resemblance with migration (e.g. animals and plants), will push a population to a highest optimum but lowest variability. In contrast, transduction of chromosome segments, a mechanism that is closer to real transduction in e.g. microorganisms, will move the population forward a highest variability but lowest optimum value (Figure 13). Both situations could represent different strategies of organisms during evolution, preventing premature convergence

(Grefenstette, 1981). The transduction of chromosome segments results in a posterior homologous recombination or crossover, promoting the sudden jump of the recipient population towards better solutions in the evolutive or fitness landscape. The explanation could be that the arrival and recombination of new genetic information (including good Holland's schemata) is breaking the population equilibrium (Gould's punctuated equilibrium; see Gould and Eldredge, 1977) in the recipient Petri dish, triggering its evolutionary change (Cohoon et al., 1987). Our findings support similar observations done in Nature. For instance, Forde et al. (2004) found evaluating the coevolution of bacterium *E. coli* and bacteriophage T7 that the local adaptation was lower in closed communities than in the open communities, suggesting that gene flow was acting as source of beneficial mutations in the open communities.

The Figure 12 shows the Multiple Box-and-Whisker Plot of the MAF_T values obtained for each one of the thirty-three types of transduction simulation experiments carried out with the AM radio receiver (*experiment 3*). The Kruskal-Wallis test shows with a *p*-value below to 2.200×10^{-16} that there are statistically significant differences among the medians at the 95.0% confidence level. Comparing the control experiment (the simulation experiment without transduction, labeled as 1 in Figure 12) with the two best transduction experiments (a chromosome segment is transferred, labeled as 19 in Figure 12, and the transference of a complete chromosome, labeled as 33 in Figure 12), we concluded as follows. No matter how is transduction the best results were obtained (Figure 13) when the donor Petri dish and bacterium (p^D, b^D) are both selected based on *max-max* criterion, being the recipients (p^R, b^R) selected with the *roul-r* criterion. Note how the best transduction protocol is the one where the simulated 'bacteriophage' selects the donor Petri dish and bacterium both with maximum fitness, such that $\max_{1,..,P}\left\{ \overline{f_1}, \overline{f_2},..., \overline{f_i} \right\}$ and $\max_{1,..,N}\left\{ f_1 , f_2 ,..., f_j \right\}$, whereas the recipients Petri dish and bacterium are both selected based on stochastic methods such as a roulette wheel approach and the uniform distribution procedure. In the Kruskal-Wallis test between the control experiment

and the transduction experiments with chromosome segments (Figure 13) the obtained *p*-value was equal to 1.603×10^{-08}. Since the *p*-value is less than 0.05 there is a statistically significant difference between the medians at the 95.0% confidence level. Of a similar way in the Kruskal-Wallis test between the control experiment and the transduction experiments with complete chromosomes (Figure 13). In such case the obtained *p*-value was below to 2.200×10^{-16}, being statistically significant the differences between the medians at the 95.0% confidence level.

In Figure 14a we show a representative performance graph (a Box-and-Whisker Plot per generation) of the control experiments (without transduction and r_e=50), as well as the graph obtained for the best transduction experiments where only chromosome segments are transferred (Figure 14b) and the transduction experiment transferring a complete chromosome (Figure 14c). Furthermore, Figure 15 shows in the aforementioned experiments the mean of the average fitness per generation (MAF). In the control experiments (Figure 15a) the MAF_T is equivalent to the $MAF_{\overline{D}\,\overline{R}}$ value per generation. Note how in transduction experiments the highest slope (Figure 15b-15c) corresponds to the donor Petri dishes (MAF_D). In such figures note the overlapping between the performance curves, thus the curve of the recipient Petri dishes (MAF_R) and the curve of the MAF value per generation calculated for all the Petri dishes (MAF_T). The oscillating behavior of MAF_R is explained considering that Petri dish and bacterium recipients are both selected applying stochastic procedures. Obviously, the worst performance is for those Petri dishes or colonies that do not participate in the transduction experiments ($MAF_{\overline{D}\,\overline{R}}$).

6. Discussion

Thirty years ago, Anderson (1970) suggested that 'virus transduction' could be considered as one of the key mechanisms of horizontal gene propagation. This fact suggests the importance of the horizontal gene transfer as evolutionary mechanism because of transporting DNA segments from individuals belonging to one phylum to individuals of another phylum. Furthermore, the evolutionary dynamic of populations could depend on the transfer of DNA from one population to other. In fact, Syvanen (1985) suggests that cross-species gene transfer could help to explain many experimental observations. For instance, the rapid bursts in evolution (Gould's punctuated equilibrium hypothesis, see Gould and Eldredge, 1977) as well as the widespread occurrence of parallelism (or convergent evolution of similar traits in the fossil record). According to Margulis (1981) the acquisition and accumulation of random mutations is not sufficient to explain how inherited variations occur. Furthermore, whereas Darwinism emphasizes the role of selection as the force behind evolution (in fact, selection is the main evolutive mechanism underlying genetic algorithms), Margulis (1981) and other evolutionary biologists emphasize the role of horizontal gene transfer and cooperation.

The simulation results are consistent with the general picture of transduction in bacteria. The transduction and conjugation operators sufficiently capture the role of such microbial genetic mechanisms in horizontal gene transfer. PETRI efficiency is shown optimizing a benchmark function, solving the 0/1 knapsack problem and evolving an optimum design of an AM radio receiver. Even when PETRI is not a distributed genetic algorithm, most DGAs and cGAs applications use a simple process of chromosome migration as only mechanism of horizontal gene transfer. However, we show how inspired in microbial genetics it is possible to develop new algorithms, genetic operators and simulation protocols that could be useful in Evolutionary Computation. For instance, in PETRI algorithm we combine two different genetic mechanisms exhibited by real bacteria. Of a side conjugation, that is a local mechanism of horizontal information

transfers *within* a population; of other transduction, thus a global mechanism of horizontal information transfers *between* populations.

In a previous paper, Kubota et al. (1996) introduced VEGA addressing the possibility to simulate transduction, a virus-evolutionary genetic algorithm. Their authors introduced a virus infection operator and a virus fitness value, modeling two populations, the host population and virus population. The main difference between this model and our model is the fact that in VEGA there are two populations: a host population representing the candidate solutions and the virus population (initially generated from host population) representing a substring set of solutions. In consequence, in VEGA the underlying model is the coevolution of two populations, a main host population and a secondary viral population. In contrast, in PETRI there are several hosts or bacterial populations (or Petri dishes) sharing solutions via transduction. Furthermore, in VEGA viruses propagate their own substrings or chromosome segments among host individuals whereas in PETRI viruses propagate only the host (or bacterial) chromosome or segments between the host individuals. Another interesting difference is that in VEGA viruses represent a real population, having each virus a fitness value. However, in our model viruses are 'dummy' agents responsible of the transduction mechanism. Finally, in VEGA the host population is not composed of bacteria since crossover is simulated as is usual in genetic algorithms, thus one-point or two-points recombination (vertical gene transfer). In contrast, PETRI simulates crossover based on a conjugation operator (horizontal gene transfer) or alternatively as VEGA, thus using one-point or two-points recombination (vertical gene transfer).

Finally, we believe that PETRI could be improved in several ways. For instance, including other features and options not considered in the present algorithm, parallelizing the algorithm to be run in a parallel computing system, or developing a routines library

based on microbial genetics, promoting the search of new horizontal gene transfer algorithms in the field of Evolutionary Computation.

Acknowledgments

We thank Bayes Forecast company for its generosity in allowing C. Perales-Graván to dedicate part of his time to participate in the present research. Rafael Lahoz-Beltra was supported by Laboratorio de Bioinformatica, Complutense Univesity of Madrid (UCM), and in part under 'Profesores UCM en el Extranjero 2008' grant.

References

Alba, E., Dorronsoro, B. (2008). *Cellular Genetic Algorithms*. Springer.

Anderson, N.G. (1970). Evolutionary significance of virus infection. *Nature*. 227: 1346-1347.

Cohoon, J. P., Martin, W.N., Richards, D.S. (1987). Punctuated equilibrium: A parallel genetic algorithm. In *Proceedings of the Fifth International Conference on Genetic Algorithms* (J.J. Grefenstette, Ed.) pages 148-154. Lawrence Erlbaum Associates, Hillsdale, NJ.

Davis, R.H., Weller, S.G. (1998). *The Gist of Genetics. Guide to Learning and Review*. Jones & Bartlett Publishers, Sudbury, MA.

Davis, B.D., Dulbecco, R., Eisen, H.N., Ginsberg, H.S. (1990). *Microbiology*. Lippincot Company, Philadelphia.

Dawkins, R. (1986). *The Blind Watch maker.* W. W. Norton & Company, Inc, New York, NY.

Elena, S.F., Lenski, R.E. (2003). Evolution experiments with microorganisms: the dynamics and genetic bases of adaptation. *Nature Genetics*. 4: 457-469.

Forde, S. E., Thompson, J. N., Bohannan, B. J. M. (2004). Adaption varies through space and time in a coevolving host-parasitoid interaction. *Nature*. 431: 841-844.

Goldberg, D.E. (1989). *Genetic Algorithms in Search, Optimization, and Machine Learning*. Addison-Wesley, Reading, MA.

Gould, S.J., Eldredge, N. (1977). Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiology* 3: 115-151.

Grefenstette, J. J. (1981). Parallel adaptive algorithms for function optimization. Tech. Rep. No. CS-81-19, Vanderbilt University, Computer Science Department, Nashville, TN.

Kubota, N., Shimojima, K., Fukuda, T. (1996). The role of virus infection in virus-evolutionary genetic algorithm. In *Proceedings of the IEEE International Conference on Evolutionary Computation*, pages 182-187. Nagoya, Japan.

Lahoz-Beltra, R. (2001). Evolving hardware as model of enzyme evolution. *BioSystems.* 61: 15-25.

Lahoz-Beltra, R. (2004). *Bioinformática: Simulación, Vida Artificial e Inteligencia Artificial* (Transl.: Spanish). Ediciones Díaz de Santos, Madrid, Spain.

Lahoz-Beltra, R. (2008). *¿Juega Darwin a los Dados?* (Transl.: Spanish). Editorial NIVOLA, Madrid, Spain.

Lahoz-Beltra R., Ochoa G., Aickelin, U. (2009). Cheating for Problem Solving: A Genetic Algorithm with Social Interactions. In *Proceedings of Genetic and Evolutionary Computation Conference (GECCO-09)*, Montreal, Canada.

Margulis, L. (1981). *Symbiosis in Cell Evolution.* W.H.Freeman & Company.

Ogunseitan, O.A. (2008). Genetic transduction in freshwater ecosystems. *Freshwater Biology*. 53: 1228-1239.

Perales-Graván, C., Lahoz-Beltra, R. (2004). Evolving morphogenetic fields in the zebra skin pattern based on Turing's morphogen hypothesis. *International Journal of Applied Mathematics and Computer Science*. 14: 351-361.

Perales-Gravan, C., Lahoz-Beltra, R. (2008). An AM radio receiver designed with a genetic algorithm based on a bacterial conjugation genetic operator. *IEEE Transactions on Evolutionary Computation*. 12(2): 129-142.

Syvanen, M. (1985). Cross-species transfer. Implications for a new theory of evolution. *Journal of Theoretical Biology*. 112: 333-343.

Swiss Federal Institute of Technology Zurich. (2008). Systems Optimization. Test Problem Suite. www.tik.ee.ethz.ch/sop/download/supplementary/testProblemSuite/

Tukey, J.W. (1977). *Exploratory Data Analysis.* Addison-Wesley, Reading, MA.

von Neumann, J. (1966). In A. Burks (Ed.), *The theory of self–reproducing automata*. University of Illinois Press, Urbana, IL.

Fig. 1. Transduction mechanism (bacterium DNA, white rectangle; bacteriophage DNA, grey rectangle). (a) Infection of a donor bacterium D with a bacteriophage. (b) Bacterial and bacteriophage DNA segments mix inside donor bacterium D. A bacterial DNA segment is packed inside the bacteriophage 'head' (c) being transferred to a recipient bacterium R. Finally, inside the recipient bacterium R homologous recombination or crossover occurs between the emigrant bacterial DNA segment and the target bacterial chromosome.

Fig. 2. Transduction operator. (a) Transferring a chromosome segment: (step a) donor bacterium D (bacterium DNA, white rectangle), (step b) recipient bacterium R (bacterium DNA, grey rectangle) and chromosome segment D' from donor bacterium, (step c) one chromosome results inside R after transduction. (b) Transferring a complete chromosome: (step a) donor bacterium D (bacterium DNA, white rectangle), (step b) recipient bacterium R (bacterium DNA, grey rectangle) and chromosome D' from donor bacterium, (step c) one chromosome results inside R after transduction. (c) Migration and crossover: (step a) donor bacterium D (bacterium DNA, white rectangle), (step b) recipient bacterium R (bacterium DNA, grey rectangle) and the migrated chromosome D' from donor bacterium, (step c) two chromosomes result inside R after migration and crossover.

Fig. 3. Bacterial conjugation operator (Perales-Gravan and Lahoz-Beltra, 2008). Once a couple of chromosomes i and j (or bacteria, D=donor, R=recipient) are selected from the same population (or Petri dish), the gene transfer occurs from a random point i_e on the donor chromosome i (O=chromosome origin). Since transfer of the donor chromosome is almost never complete then the length ℓ of the strand (a copy) transferred to the recipient cell R is simulated applying Monte Carlo method, assuming DNA lengths exponentially distributed with a parameter α (conjugation parameter). Finally, the transferred strand experiences crossover, resulting a recombinant chromosome j in bacterium R.

Fig.4. AM radio receiver. (a) Electronic circuit of a simple crystal radio showing the main electronic components to be optimized. (b) Radio enclosure details. (c) Bacterial chromosome with 14 genes codifying for the main characteristics of an AM radio receiver (from Perales-Gravan and Lahoz-Beltra, 2008).

Fig. 5. Horizontal gene transfer (HGT) mechanisms in bacteria. Conjugation is a mechanism of HGT *within* population, whereas transduction is a HGT mechanism *between* populations.

Fig. 6. Transduction experiment. The figure shows transduction from donors' Petri dish (p^D) and bacterium (b^D) to recipients Petri dish (p^R) and bacterium (b^R). In the figure, P is the total number of Petri dishes (or sub-populations), N is the number of bacteria (or population size) per Petri dish and r_e the number of experimental replicates.

Fig. 7. Multiple bacterial colonies (or Petri dishes) are communicated via bacteriophages, cycling through generations searching for an optimum solution during G generations.

Fig. 8. SDS protocol (for details see text).

Fig. 9. AM radio receiver experiment with transduction transferring chromosome segments. Note how this kind of simulation experiment is an example of specialized transduction, where only three possible chromosome segments could be transferred by bacteriophages (for explanation see text).

Fig. 10. Michalewicz function experiments with transduction transferring complete chromosomes. The figure shows the medians (notches) and MAF (crosses) of the average

fitness values obtained in fifteen different simulation experiments: Conjugation with p_t equal to 0% (without transduction) (1), 25% (2), 50% (3), 75% (4) and 100% (5). One-point recombination with p_t equal to 0% (without transduction) (6), 25% (7), 50% (8), 75% (9) and 100% (10). Two-points recombination with p_t equal to 0% (without transduction) (11), 25% (12), 50% (13), 75% (14) and 100% (15).

Fig. 11. Knapsack problem experiments with transduction transferring complete chromosomes. The figure shows the medians (notches) and MAF (crosses) of the maximum fitness values obtained in fifteen different simulation experiments: Conjugation with p_t equal to 0% (without transduction) (1), 25% (2), 50% (3), 75% (4) and 100% (5). One-point recombination with p_t equal to 0% (without transduction) (6), 25% (7), 50% (8), 75% (9) and 100% (10). Two-points recombination with p_t equal to 0% (without transduction) (11), 25% (12), 50% (13), 75% (14) and 100% (15).

Fig. 12. Multiple Box-and-Whisker Plot for the AM radio receiver problem. The figure shows the medians (notches) and MAF (crosses) of the average fitness values obtained in thirty-three different simulation experiments (donor Petri dish - donor bacterium, recipient Petri dish - recipient bacterium). The following experiments were carried out transferring chromosome segments with p_t equal to 100%: (1) Control experiment (without transduction). (2) *r-r*, *r-r*. (3) max-max, max-max. (4) *ave-ave*, *ave-ave*. (5) roul-roul, roul-roul. (6) *min-min*, *min-min*. (7) *inv roul-inv roul*, *inv-roul-inv roul*. (8) *roul-roul* , *min-min*. (9) *roul-roul*, *ave-ave*. (10) *roul-roul*, *inv-roul-inv roul*. (11) *roul-roul*, *max-max*. (12) *roul-roul*, *r-r*. (13) *min-min*, *roul-roul*. (14) *ave-ave*, *roul-ro*ul. (15) *inv roul-inv roul*, *roul-roul*. (16) *max-max*, *roul-roul*. (17) *r-r*, *roul-roul*. (18) *max-max*, *roul-roul*. (19) *max-max*, *roul-r*. (20) *max-max*, *roul-min*. (21) *max-max*, *roul-ave*. (22) *max-max*, *roul-max*. (23) *max-max* , *roul-inv roul*. (24) *max-max*, *max-roul*. (25) *max-max*, *max-r*. (26) *max-max*, *max-min*. (27) *max-max*, *max-ave*. (28) *max-max*, *max-inv roul*. Experiments transferring chromosome segments with p_t equal to: (29) 75% and *max-*

max, roul-r, (30) 50% and *max-max, roul-r*, (31) 25% and *max-max, roul-r*, (32) 0% and *max-max, roul-r*. Finally, experiment (33) was carried out transferring a complete chromosome with p_t equal to 100% and *max-max, roul-r*.

Fig. 13. Multiple Box-and-Whisker Plot for the AM radio receiver problem. The figure shows the medians (notches) and MAF (crosses) of the average fitness values obtained in the (a) control experiment (without transduction) and the two best transduction experiments: (b) *max-max, rul-r* (transferring chromosome segments). (c) *max-max, rul-r* (transferring a complete chromosome).

Fig. 14. Representative performance graph for the AM radio receiver problem showing the Box-and-Whisker Plot per generation: (a) control experiment (without transduction) and the two best transduction experiments: (b) *max-max, rul-r* (transferring chromosome segments). (c) *max-max, rul-r* (transferring a complete chromosome).

Fig. 15. Performance graph for the AM radio receiver problem: (a) control experiment (without transduction) showing the mean of the average fitness per generation for the total of Petri dishes (MAF_T). The performance graph in the two best transduction experiments: (b) *max-max, rul-r* (transferring chromosome segments) and (c) *max-max, rul-r* (transferring a complete chromosome) showing MAF_T (thick and gray line), MAF_D (dashed line), MAF_R (peaks and valleys line) and $MAF_{\overline{DR}}$ (solid line) values.

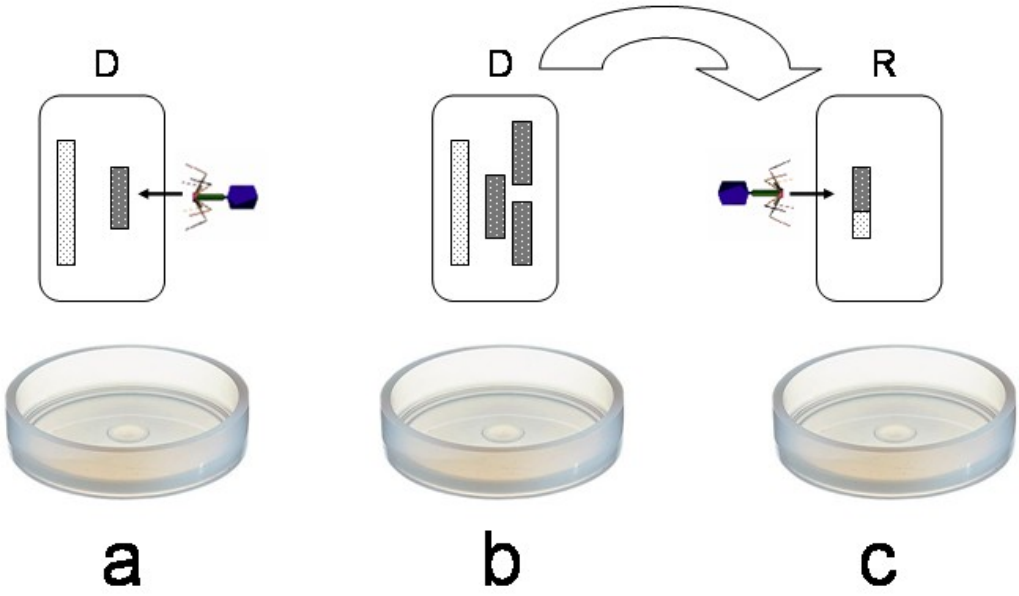

Figure 1

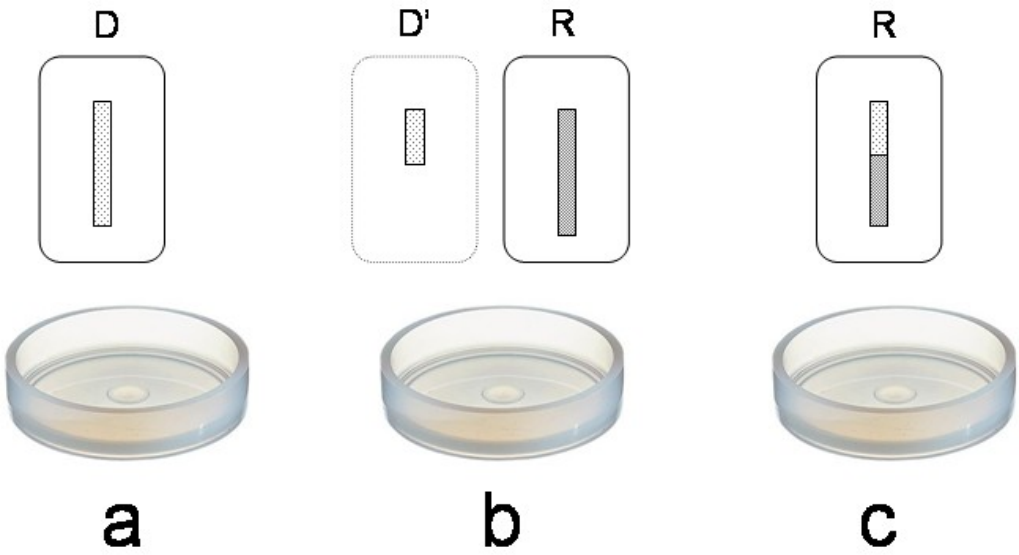

Figure 2a

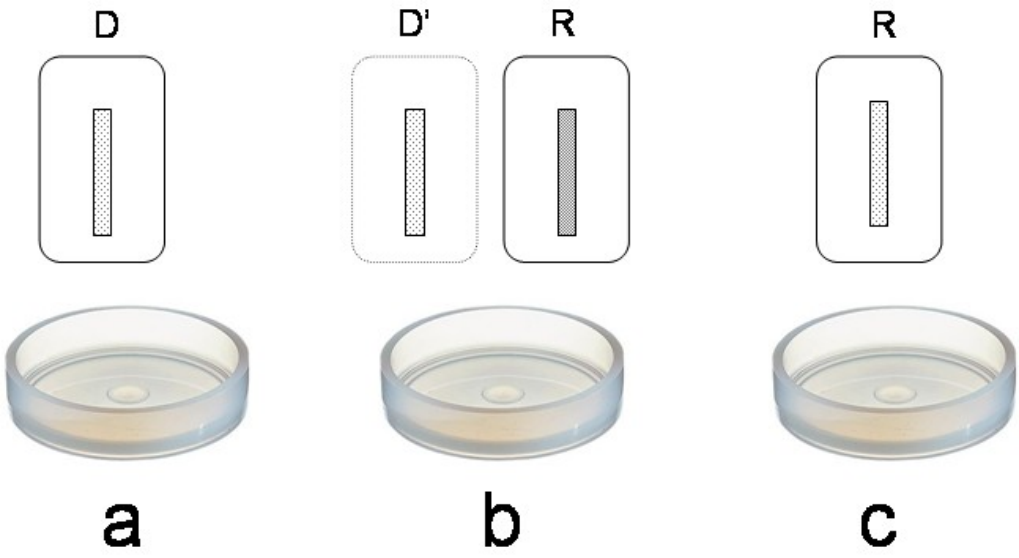

Figure 2b

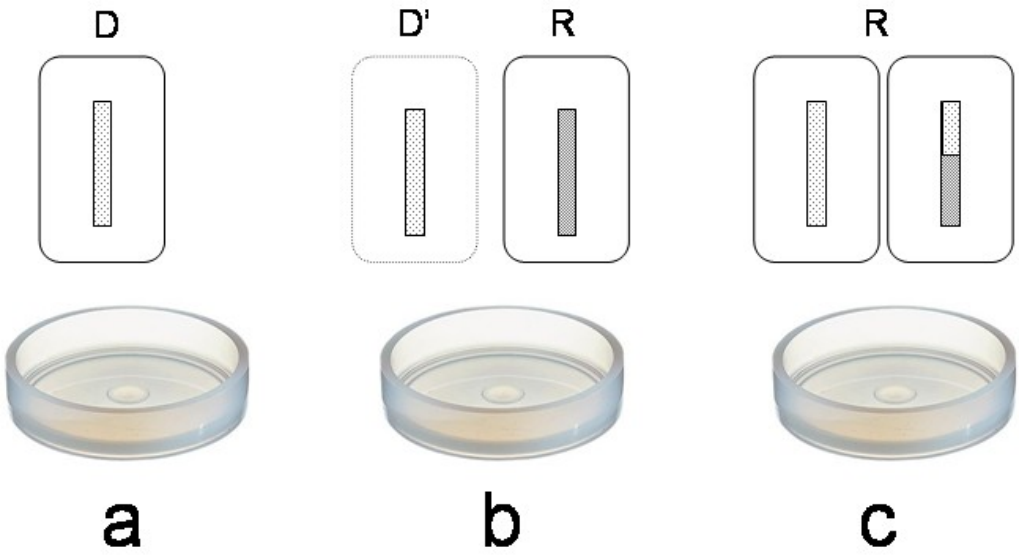

Figure 2c

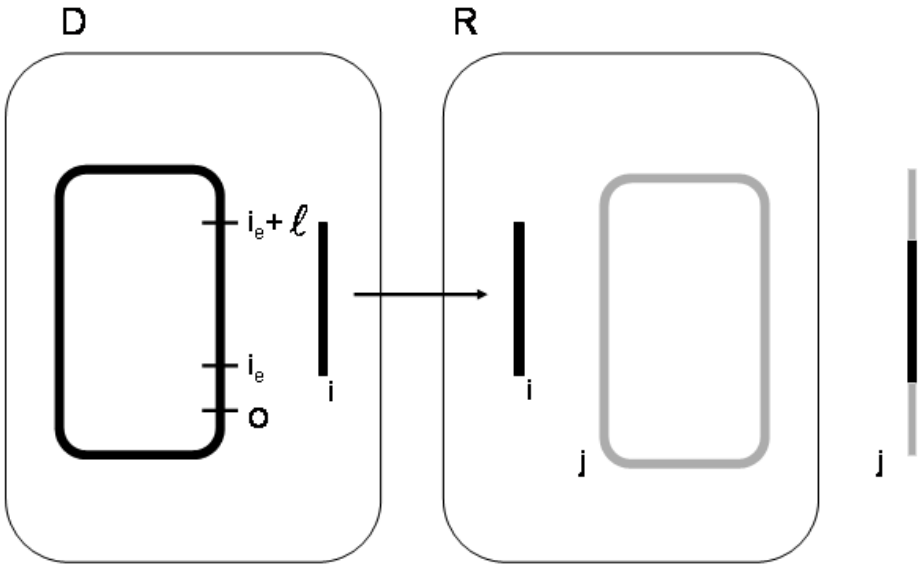

Figure 3

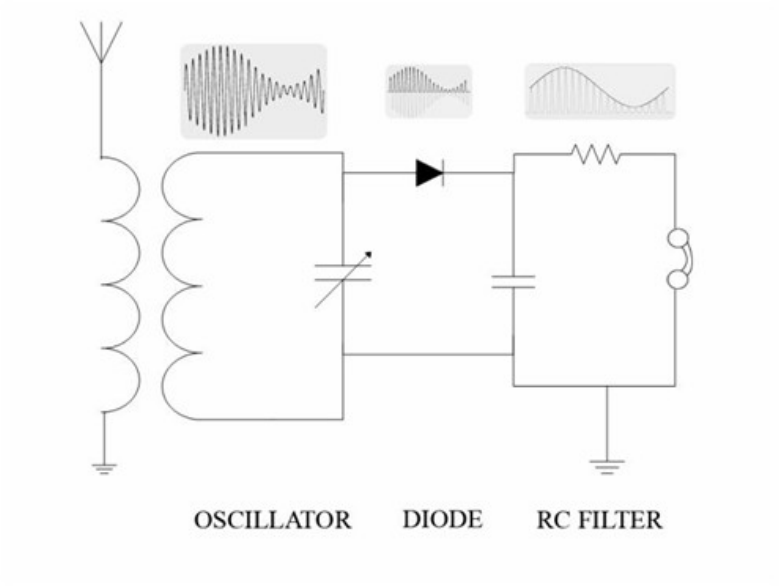

Figure 4a

Figure 4b

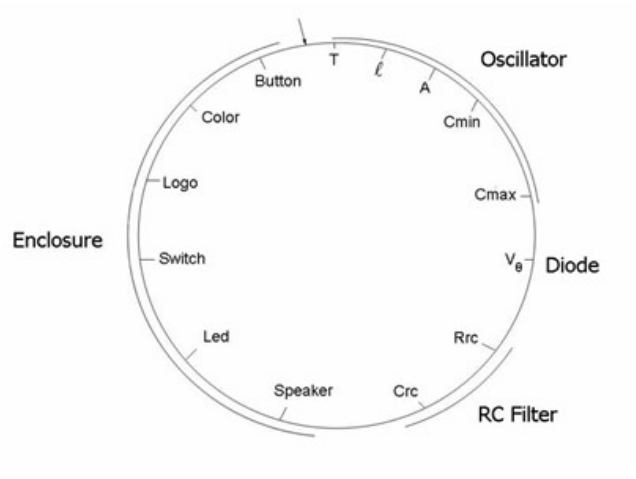

Figure 4c

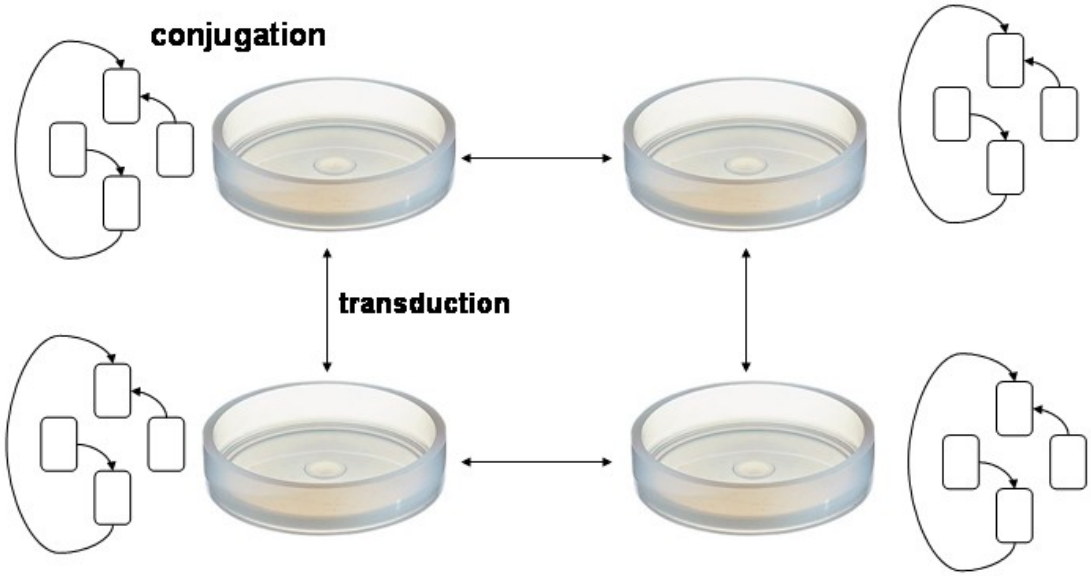

Figure 5

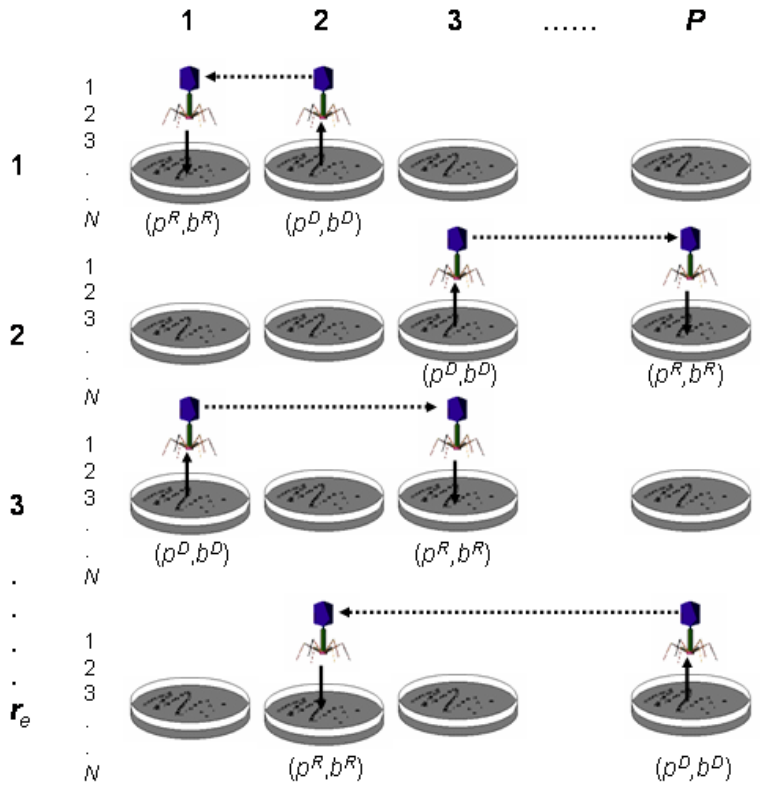

Figure 6

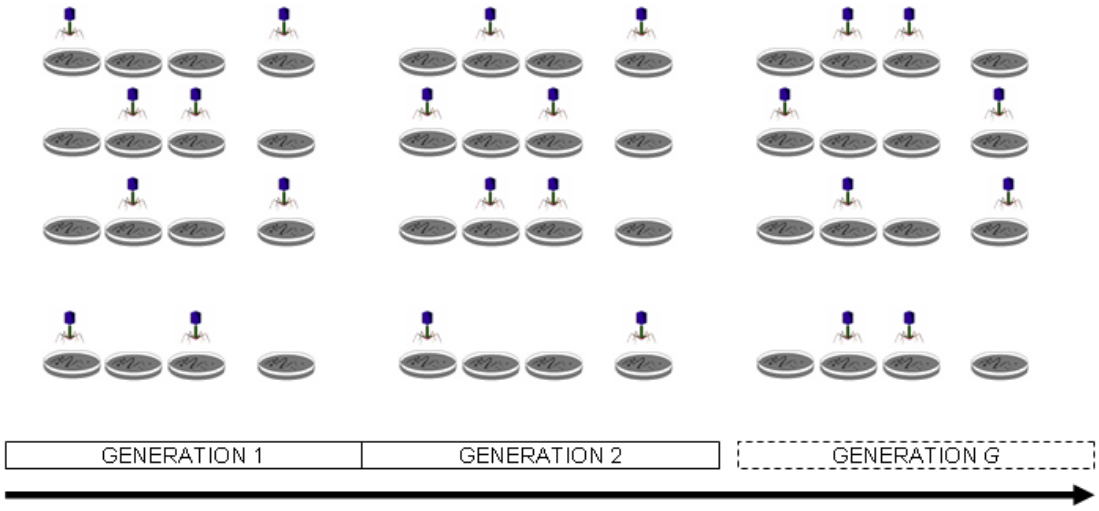

Figure 7

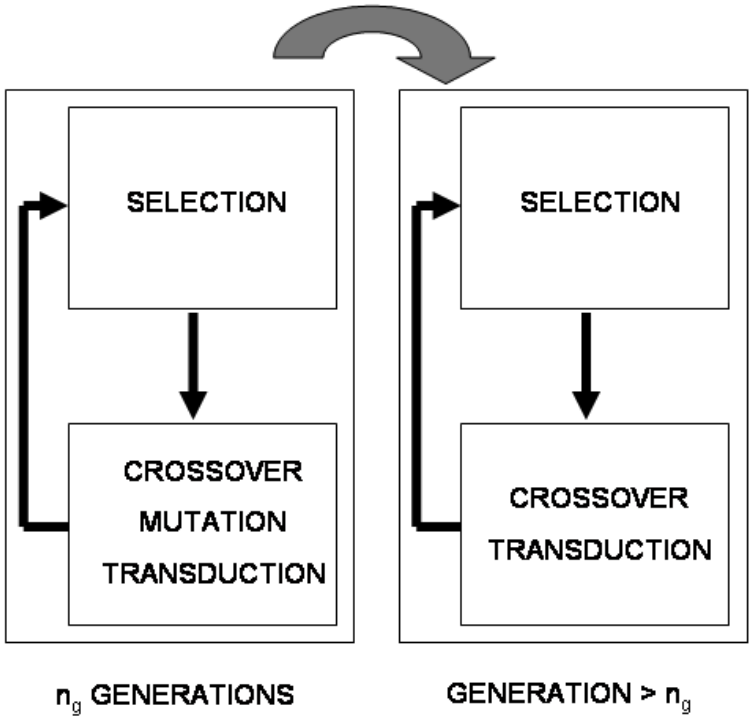

Figure 8

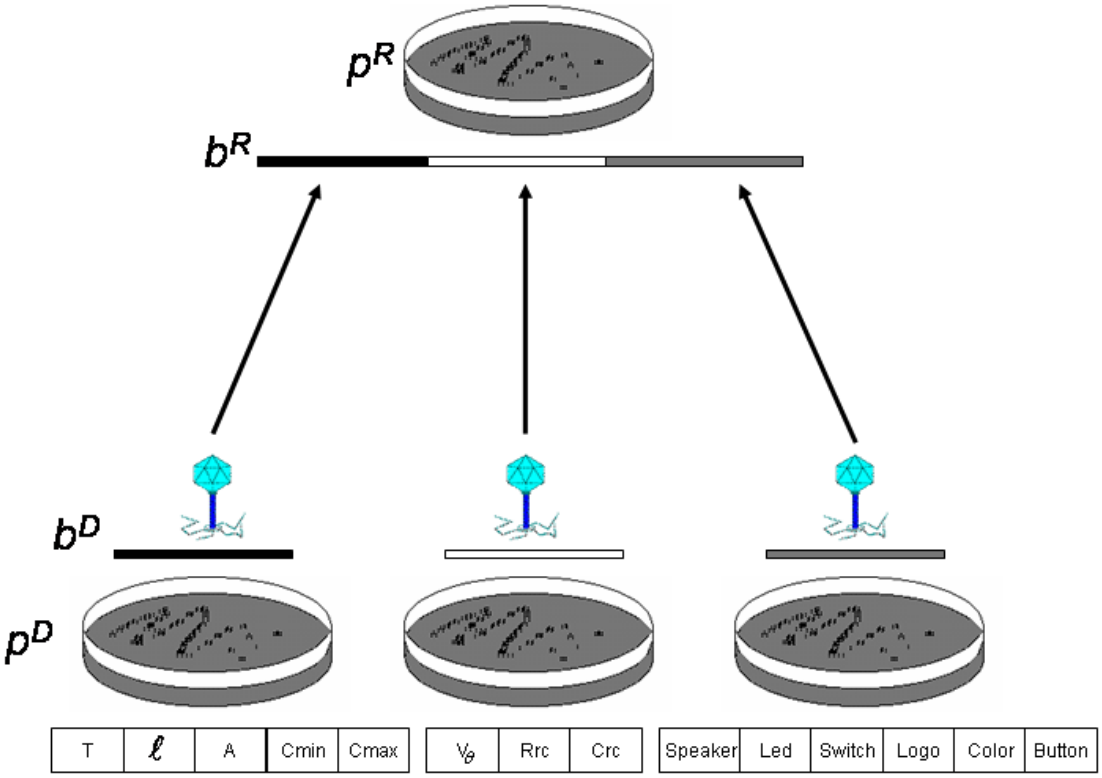

Figure 9

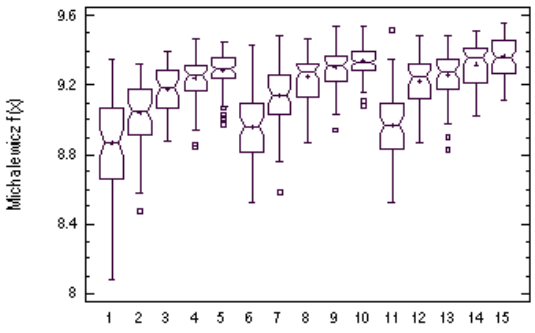

Figure 10

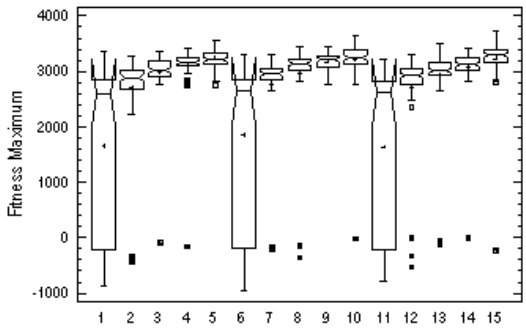

Figure 11

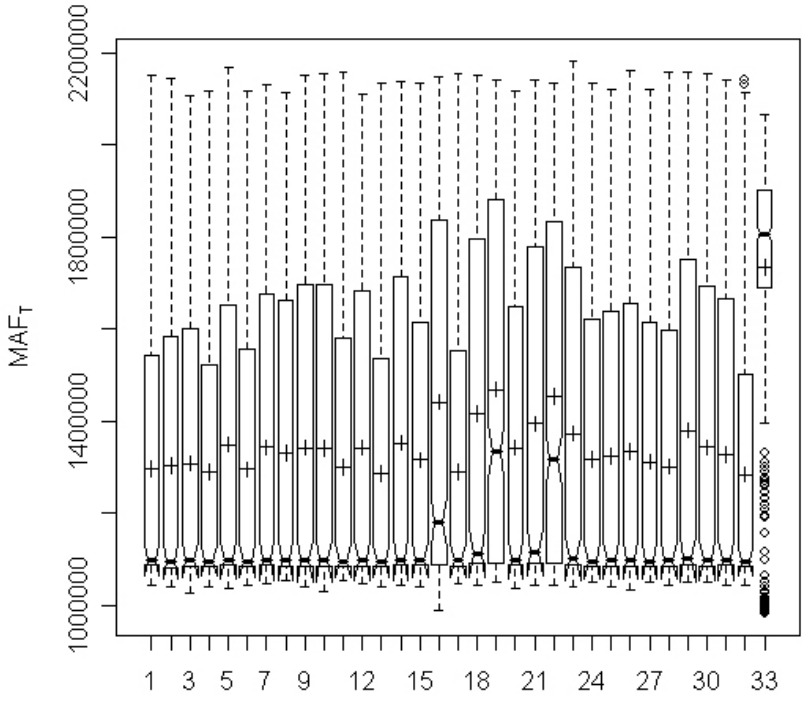

Figure 12

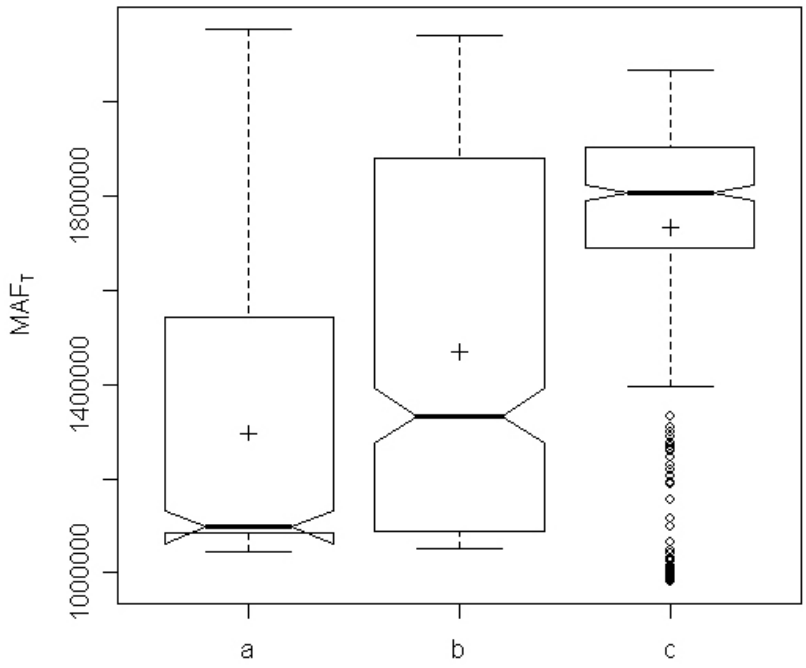

Figure 13

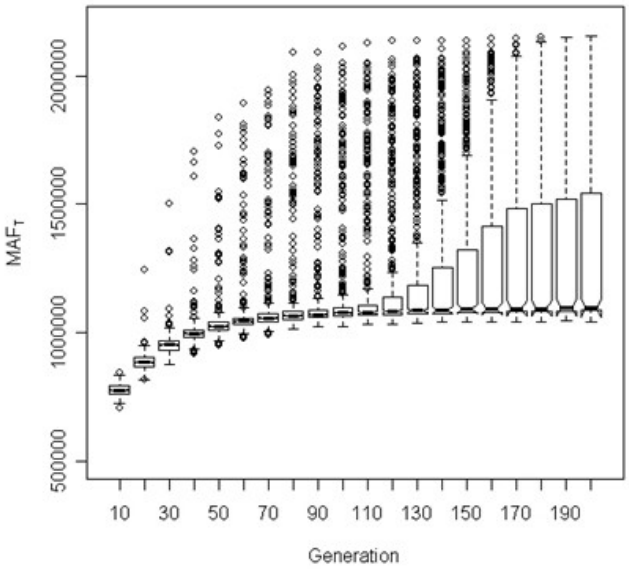

Figure 14a

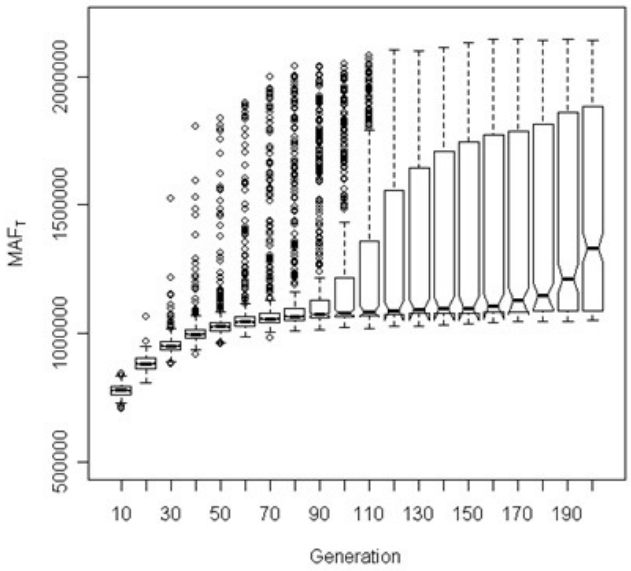

Figure 14b

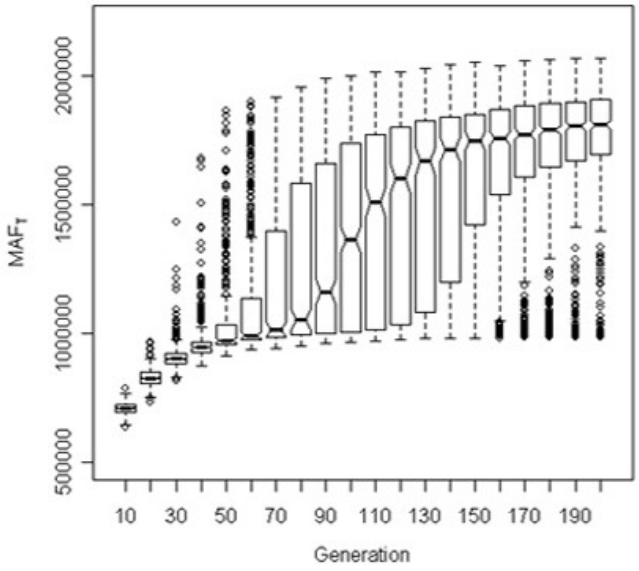

Figure 14c

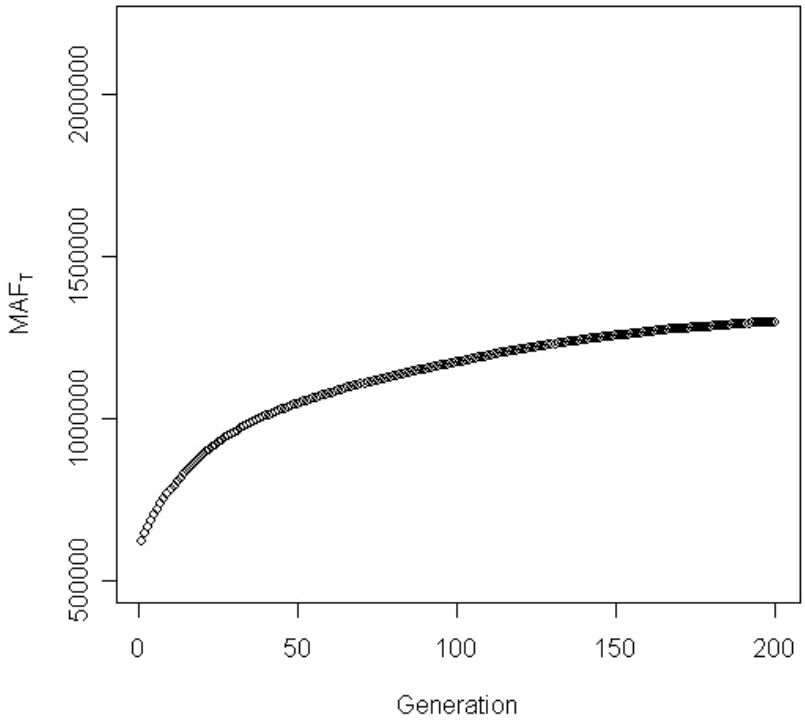

Figure 15a

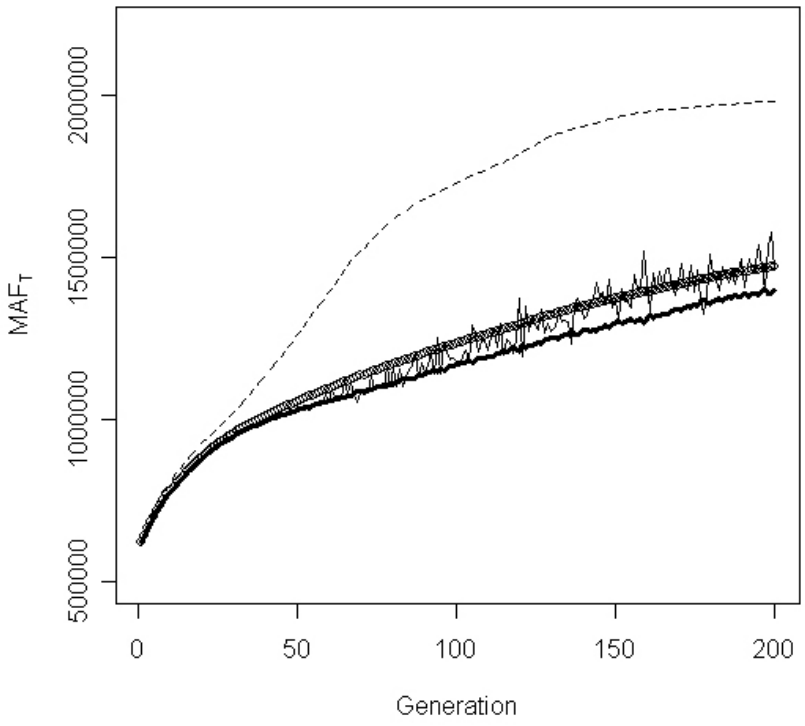

Figure 15b

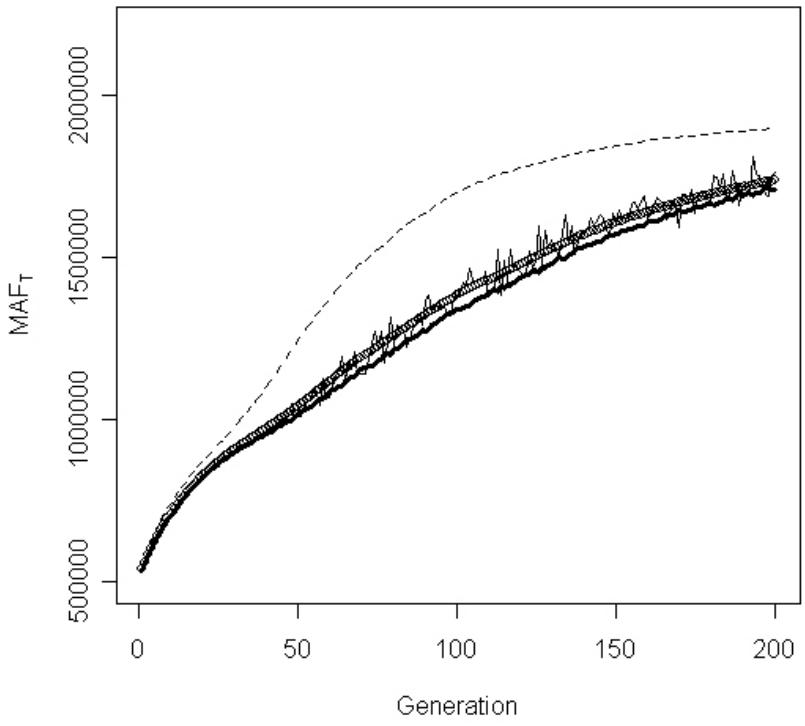

Figure 15c