Forward-time simulations using simuPOP, a tutorial

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simuPOP workshop
School of Public Health, Department of Biostatistics
University of Alabama Birmingham

outline

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2 Dive into simuPOP

3 More examples

4 Bundled Scripts

Outline

What is simuPOP

Forward- and backward-time simulation

Applications of forward-time simulations

Features of simuPOP

Availability

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1 What is simuPOP

- Forward- and backward-time simulation
- Applications of forward-time simulations
- Features of simuPOP
- Availability

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A forward-time population genetics simulation environment

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A forward-time population genetics simulation environment

- A population genetics simulation program

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A forward-time population genetics simulation environment

- A population genetics simulation program
- Not coalescent-based

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A forward-time population genetics simulation environment

- A population genetics simulation program
- Not coalescent-based
- Based on an object-oriented scripting language (Python)

Forward-time simulation

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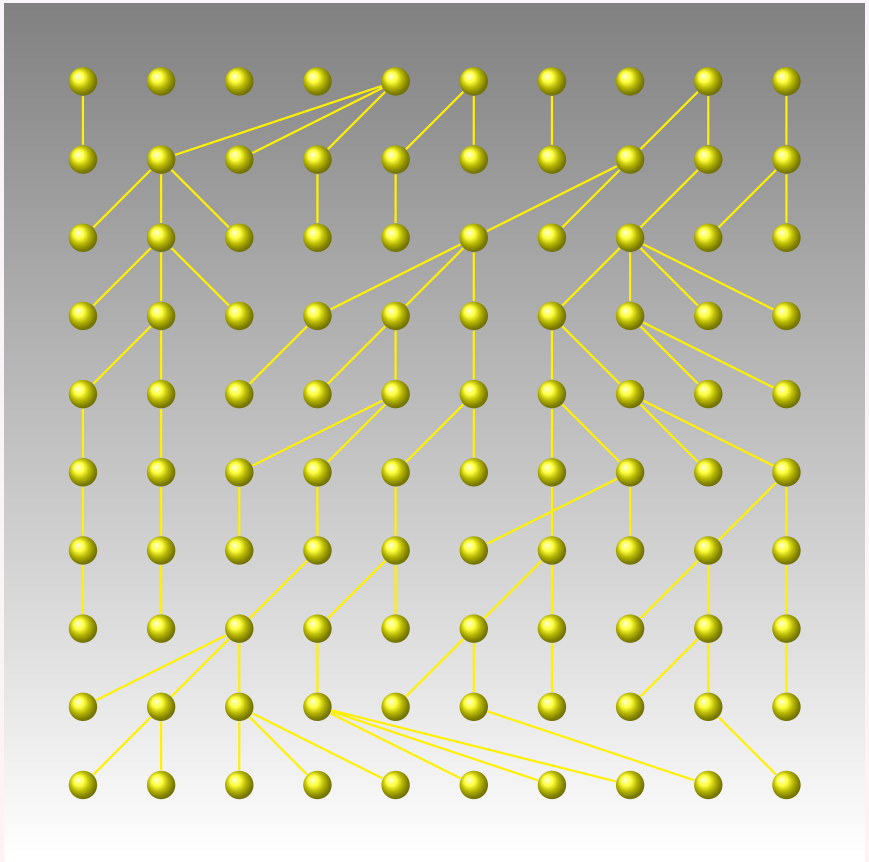

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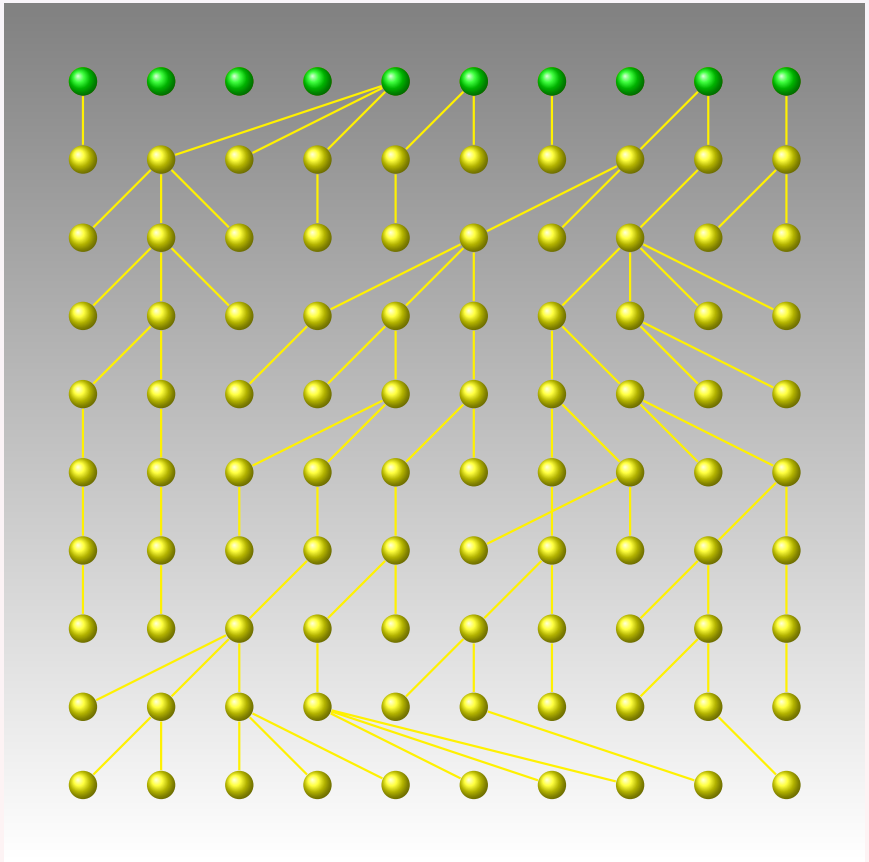

- Start from an initial population

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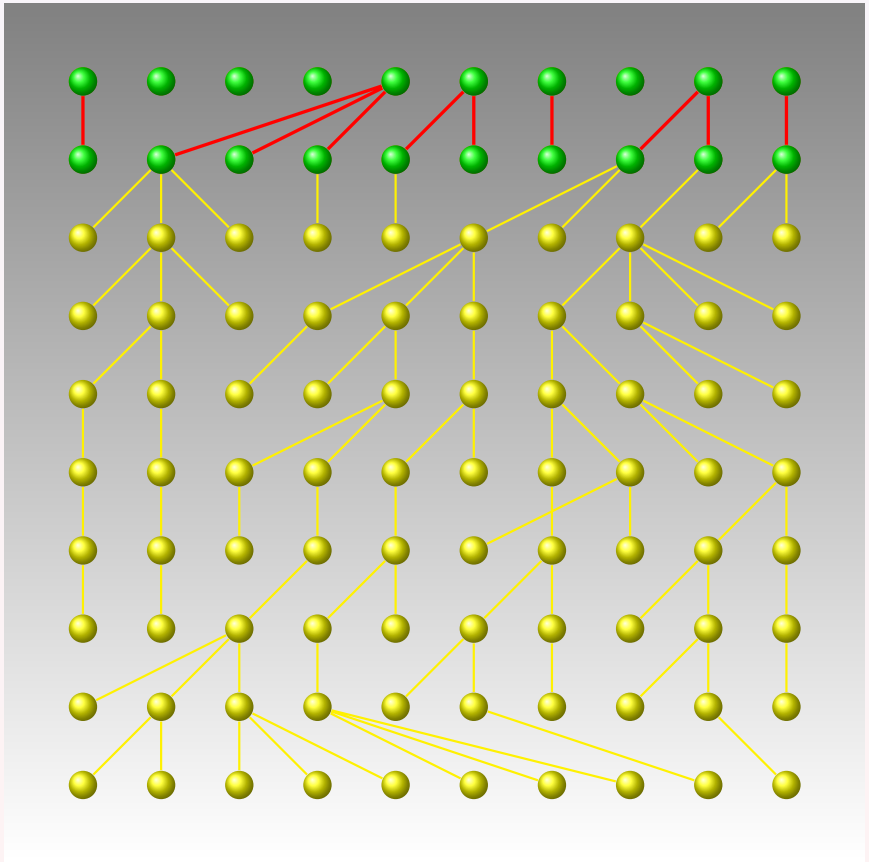

- Start from an initial population
- Evolve forward in time, generation by generation, subject to certain number of genetic and/or demographic effects

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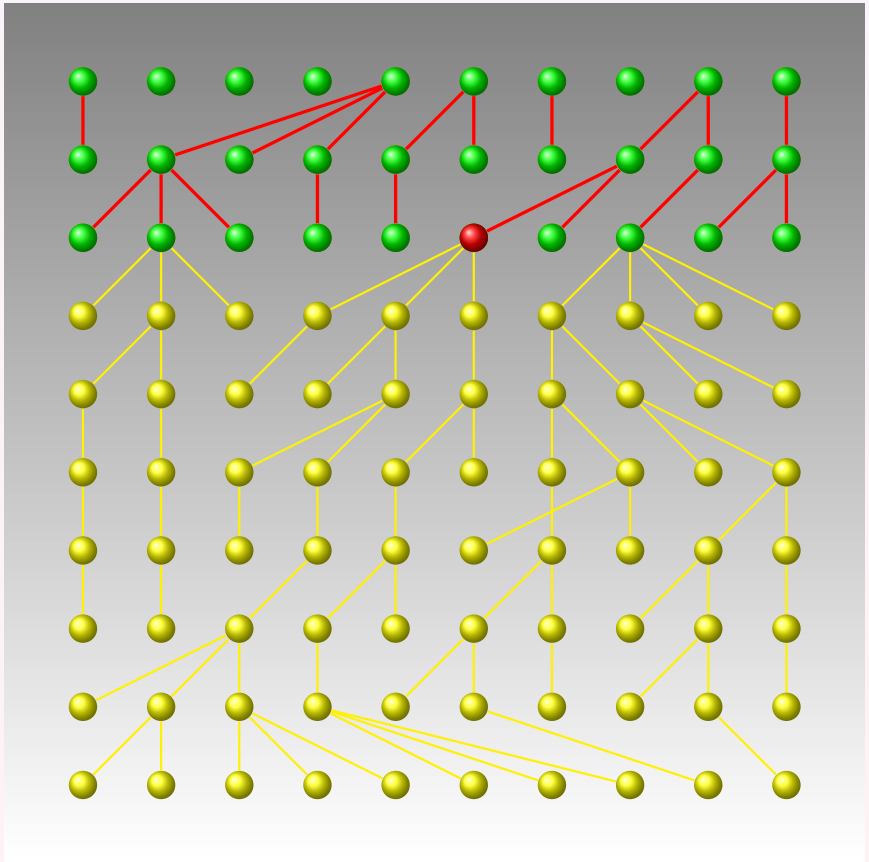

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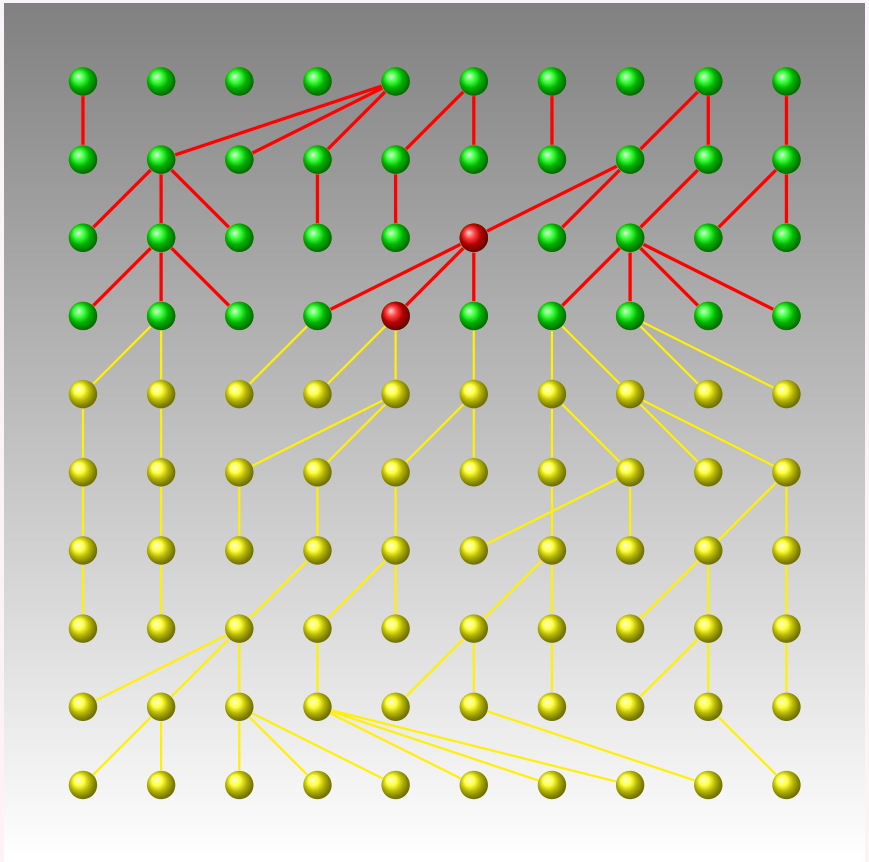

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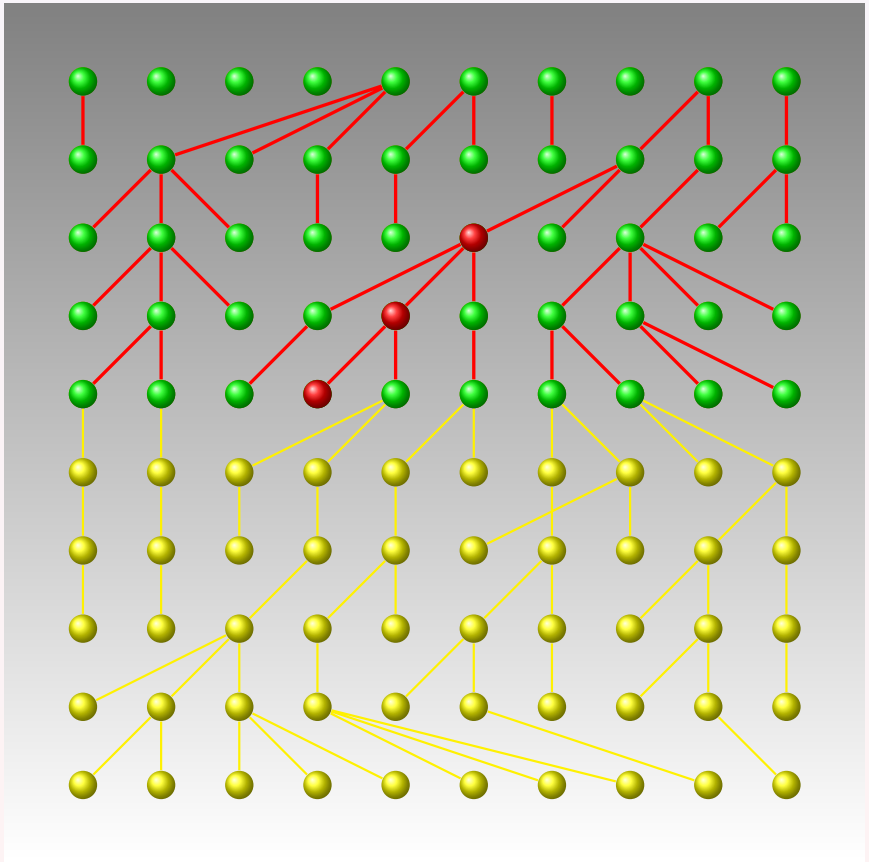

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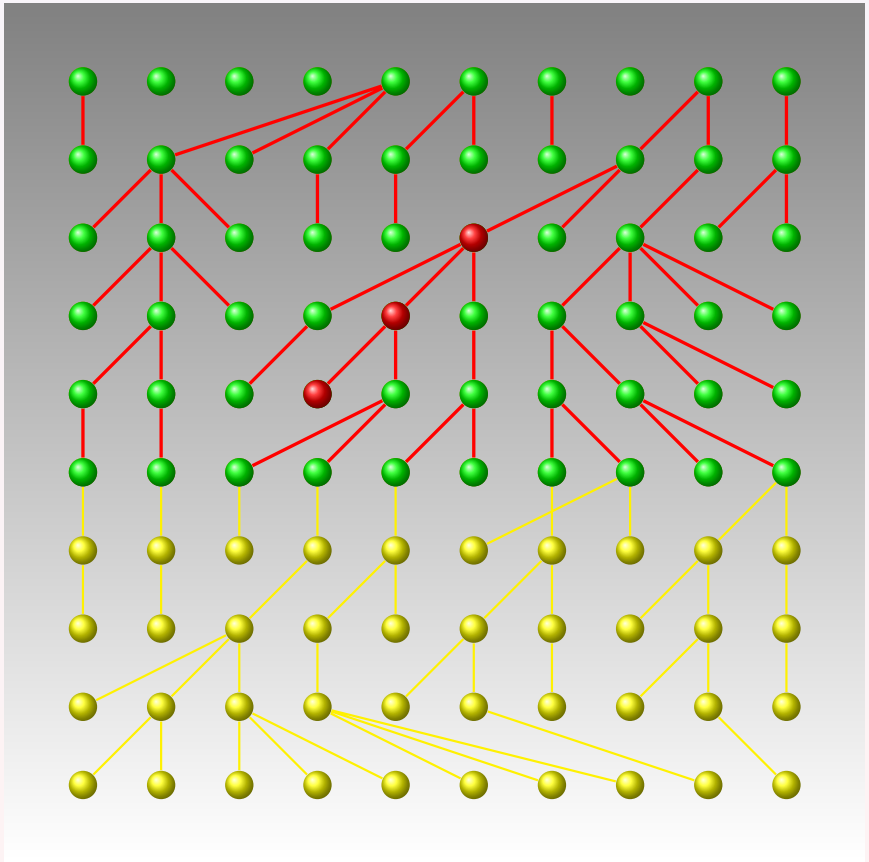

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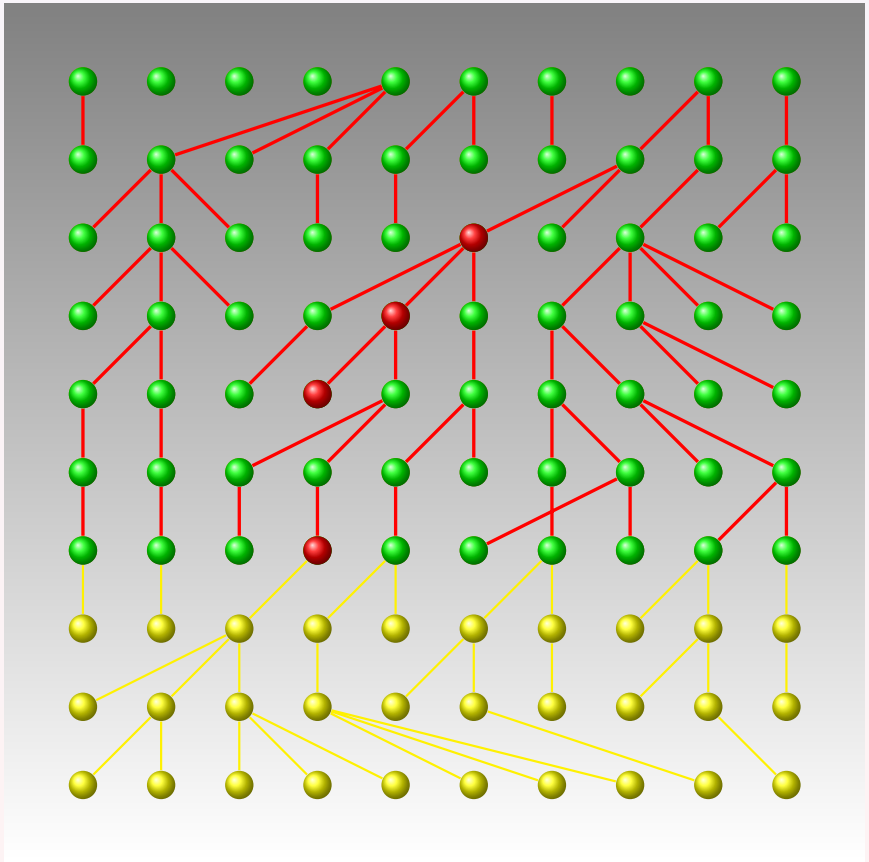

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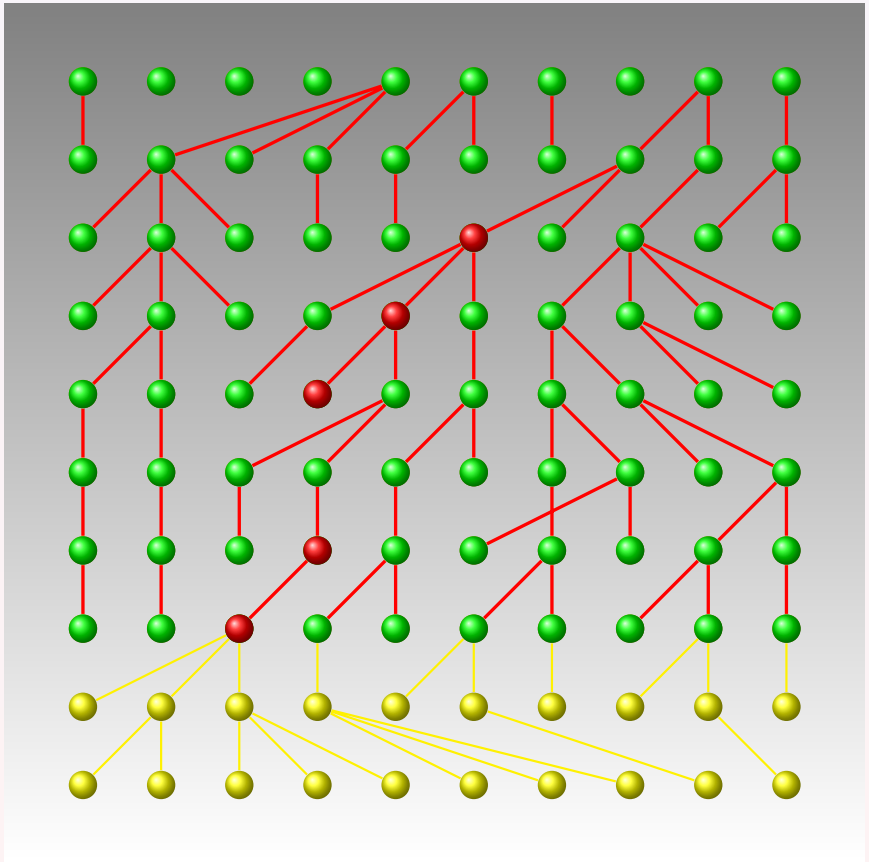

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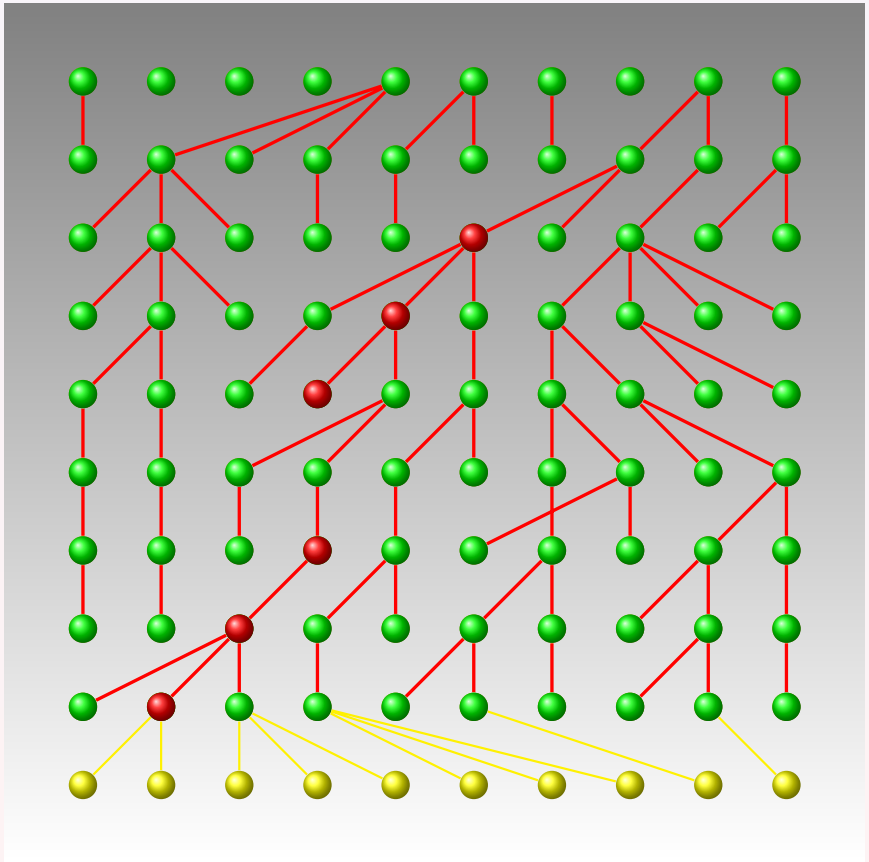

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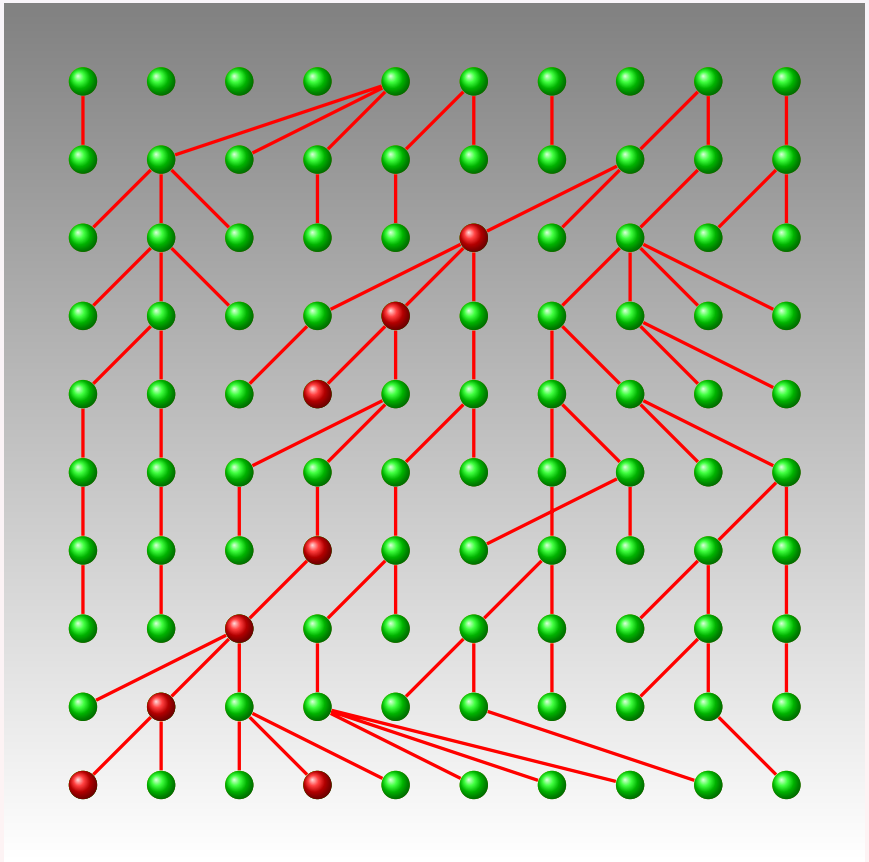

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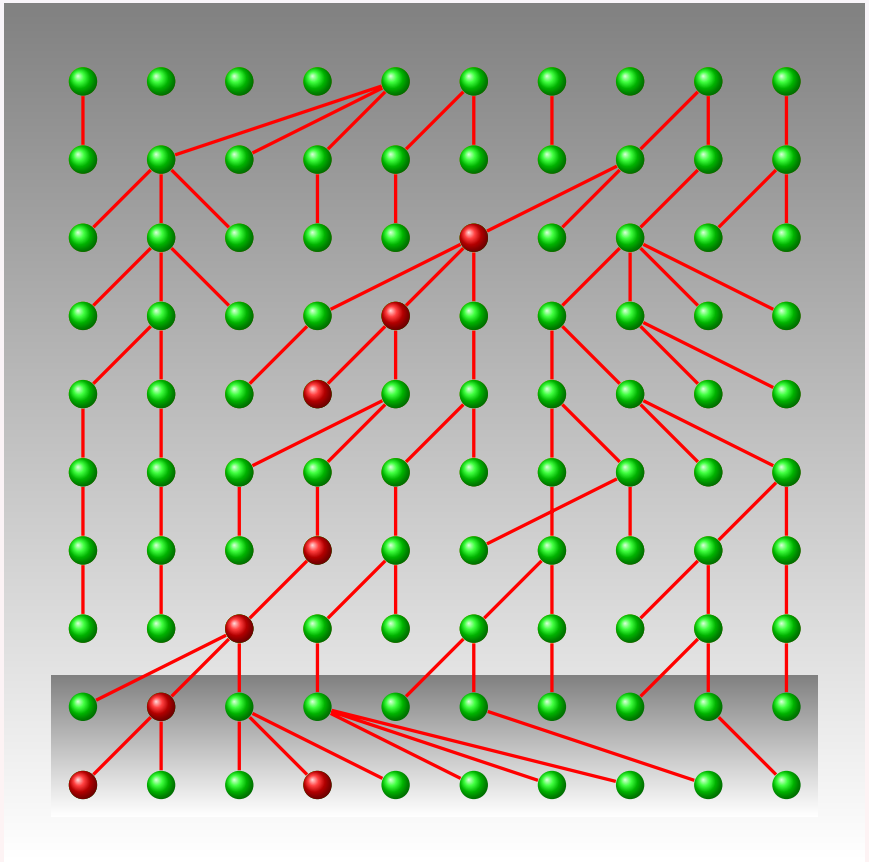

- Start from an initial population
- Evolve forward in time, generation by generation, subject to certain number of genetic and/or demographic effects
- Samples are collected from the last several generations

Backward-time simulation

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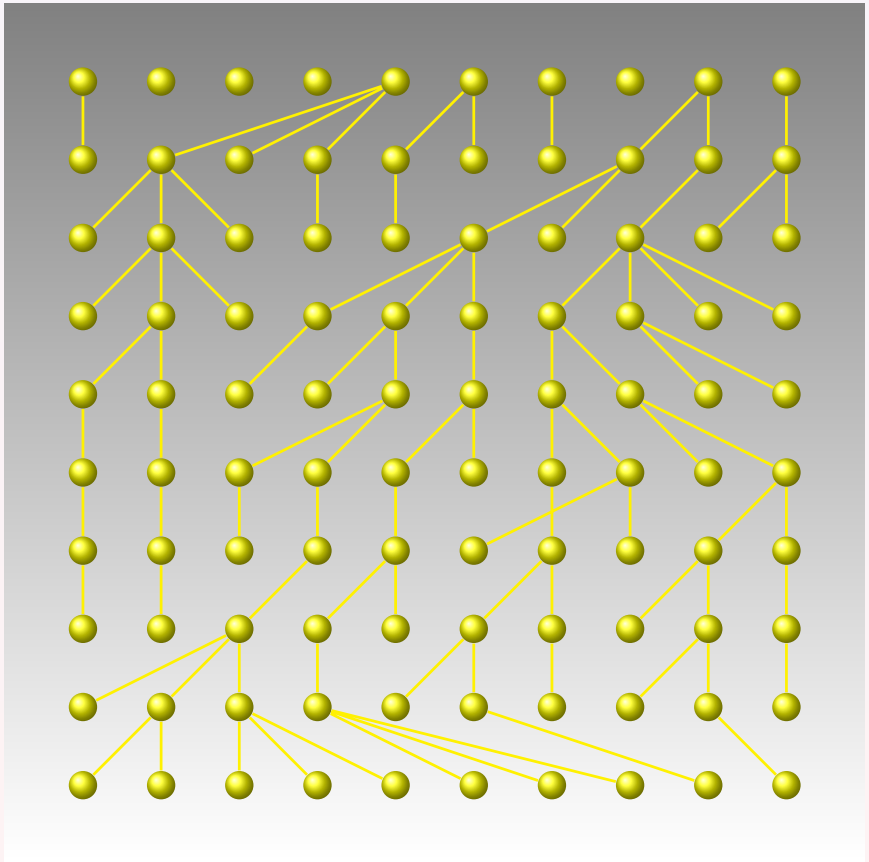

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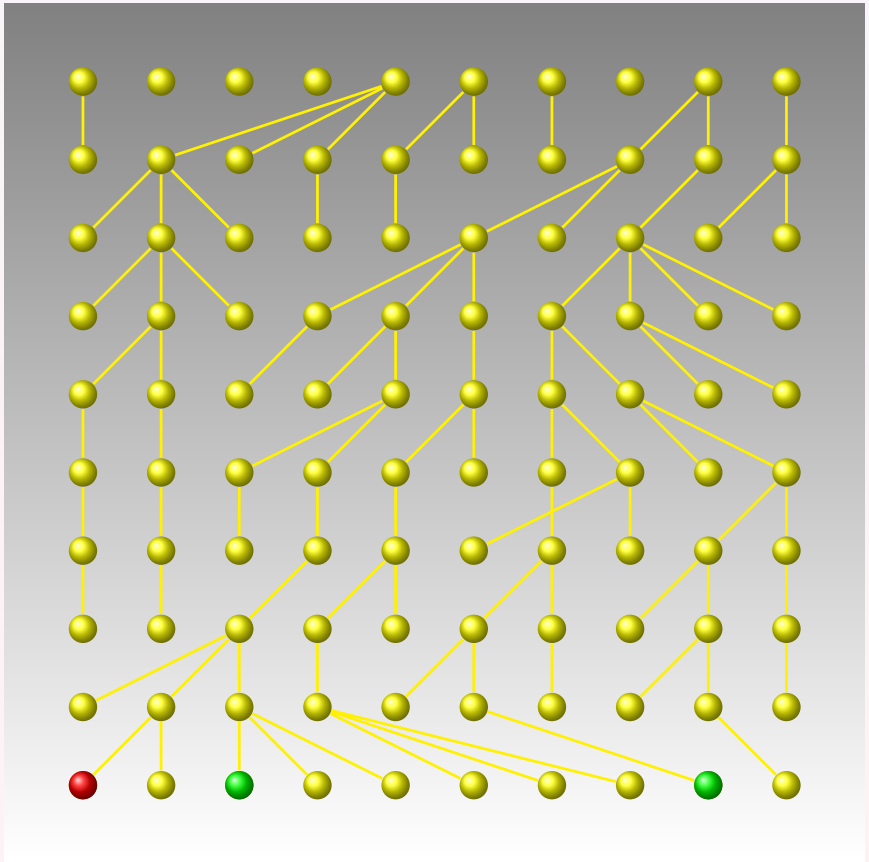

- Start from a sample with unknown genotypes

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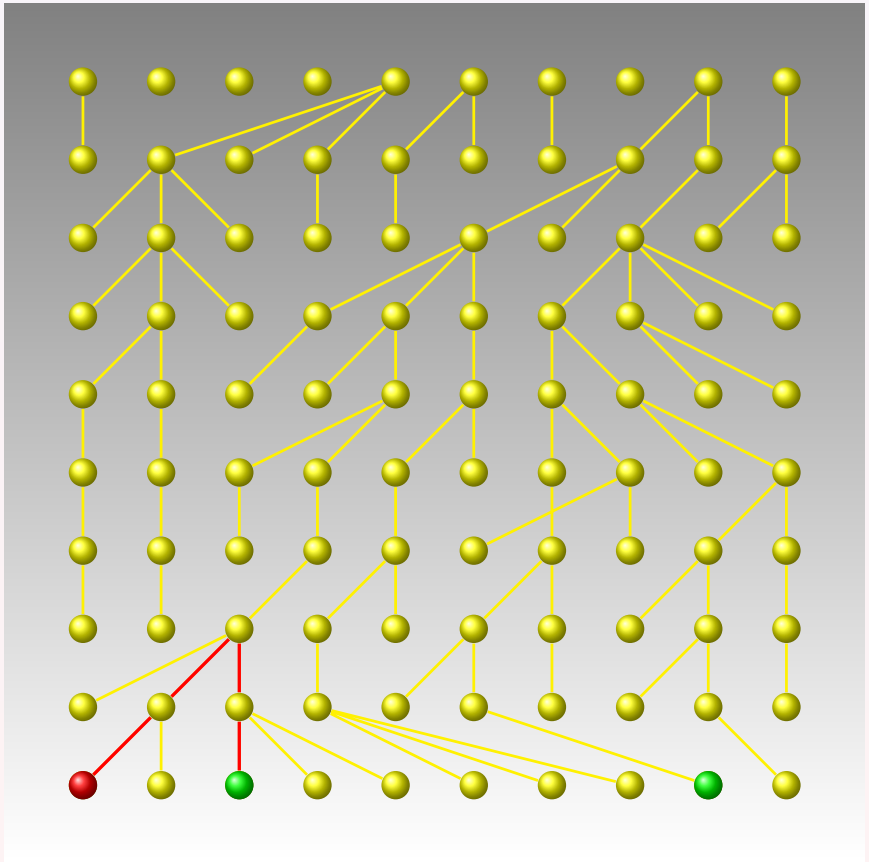

- Start from a sample with unknown genotypes
- Coalesce individuals until the most recent common ancestor of all individuals is found

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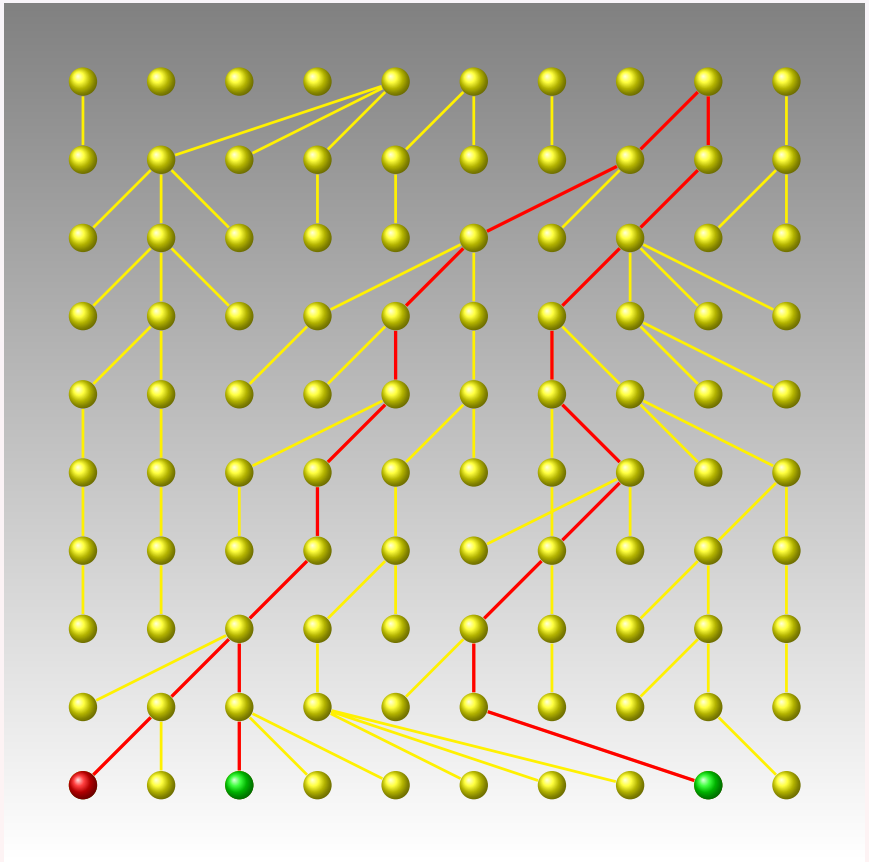

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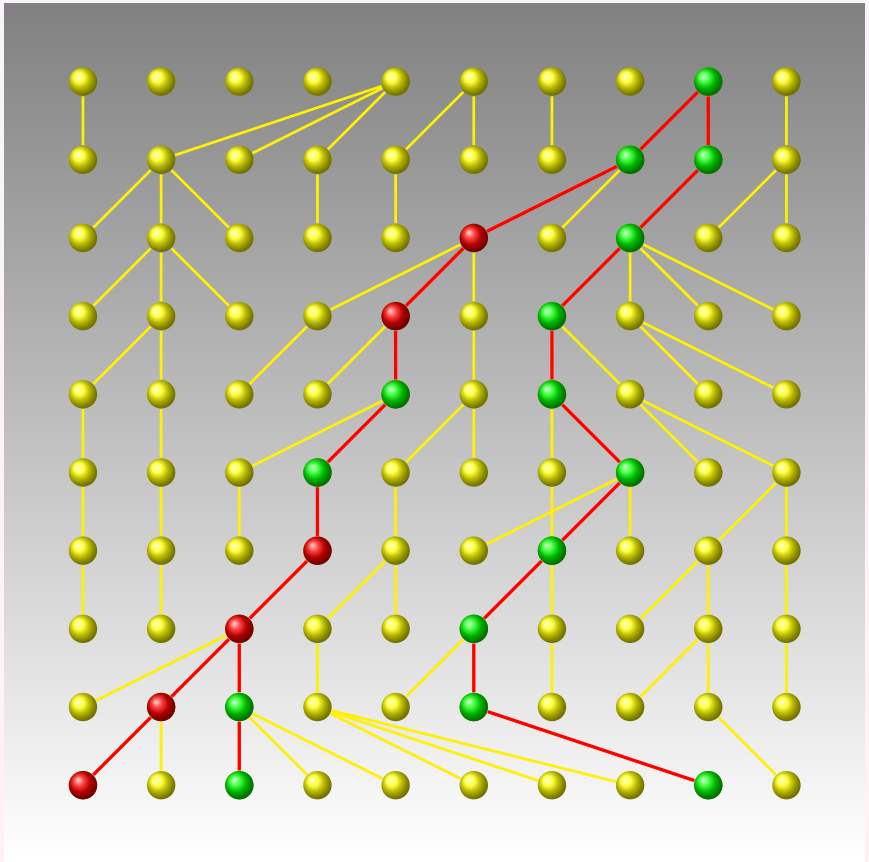

- Start from a sample with unknown genotypes
- Coalesce individuals until the most recent common ancestor of all individuals is found
- Starting from the MRCA, proceed forward in time and fill the genotype of each individual

Forward vs. backward-time simulations

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Backward-time

- Sample based, efficient

Forward-time

- Population based, inefficient

Forward vs. backward-time simulations

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Backward-time

- Sample based, efficient
- Limited selection, recombination models and mating schemes

Forward-time

- Population based, inefficient
- Can simulate almost arbitrary evolutionary scenarios

Forward vs. backward-time simulations

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Backward-time

- Sample based, efficient
- Limited selection, recombination models and mating schemes
- Can not study population properties, or properties of ancestral generations

Forward-time

- Population based, inefficient
- Can simulate almost arbitrary evolutionary scenarios
- Can study population properties and ancestral generations

Forward vs. backward-time simulations

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Backward-time

- Sample based, efficient
- Limited selection, recombination models and mating schemes
- Can not study population properties, or properties of ancestral generations
- Used mostly for sample generation

Forward-time

- Population based, inefficient
- Can simulate almost arbitrary evolutionary scenarios
- Can study population properties and ancestral generations
- Not limited to sample generation

Applications of forward-time simulations

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simuPOP can simulate the change of the genetic composition of a population in a complicated evolutionary process. It can be used to

- Demonstrate population genetics phenomena

Applications of forward-time simulations

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simuPOP can simulate the change of the genetic composition of a population in a complicated evolutionary process. It can be used to

- Demonstrate population genetics phenomena
- Study the impact of genetic and demographic forces on the evolution of a population

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- Simulate samples to validate gene-mapping methods

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Specific topics

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Discipline	Topic	Feasibility
Epidemiology	Disease risk in population	OK
	Complex sample features	OK
Evolutionary Biology and Genetics	Drift, mutation, selection, recombination, migration, subpopulation	OK
Statistical Genetics	Disease data for linkage analysis	OK
	Gene Network	Not sure
	Haplotype inference	OK
	Copy number variation	Not sure
	Time series	Not sure
	Spatial fields	Limited
Ecology etc	Animal line-breeding	Limited

Simulations of complex human diseases

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Backward-time

- Haploid only

Forward-time

- No limit on ploidy

Simulations of complex human diseases

Backward-time

- Haploid only
- Additive selection and penetrance models

Forward-time

- No limit on ploidy
- Arbitrary selection and penetrance models

Simulations of complex human diseases

Backward-time

- Haploid only
- Additive selection and penetrance models
- One disease susceptibility locus

Forward-time

- No limit on ploidy
- Arbitrary selection and penetrance models
- Multiple DSL with interaction

Simulations of complex human diseases

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Backward-time

- Haploid only
- Additive selection and penetrance models
- One disease susceptibility locus
- Generate independent samples of fixed format

Forward-time

- No limit on ploidy
- Arbitrary selection and penetrance models
- Multiple DSL with interaction
- Generate multi-generation populations

Forward-time simulation programs

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For specific applications

- Easy to write simple simulations (C++, Perl, ...)
- Difficult to write complicated simulations
- A few programs are available (e.g. EasyPOP, FPG, Nemo), easy to use if they happen to fit your need

Forward-time simulation programs

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For general purposes

- Difficult to write
- Easy to set up complicated simulations
- simuPOP fits in this category

What simuPOP does

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simuPOP provides

- a large number of functions to manipulate populations
  copy, split, merge, manipulate individual genotypes, determine affection status, save to and load from various formats, generate sample, ...

What simuPOP does

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simuPOP provides

- a large number of functions to manipulate populations copy, split, merge, manipulate individual genotypes, determine affection status, save to and load from various formats, generate sample, ...
- and a mechanism to evolve populations forward in time subject to arbitrary demographic and genetic forces such as population size changes, mutation, migration, recombination, selection, ...

Structure of individuals

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Assume ploidy = 2, maxAllele = 1

0	1	2		3	4			5	6
0	1	1		1	0			0	1
0	0	1		1	1			0	1

0			1	2	3	4	5
0			1	0	0	0	1
1			0	1	1	0	0

Male

- Affected

fitness	father_idx	...

Structure of individuals

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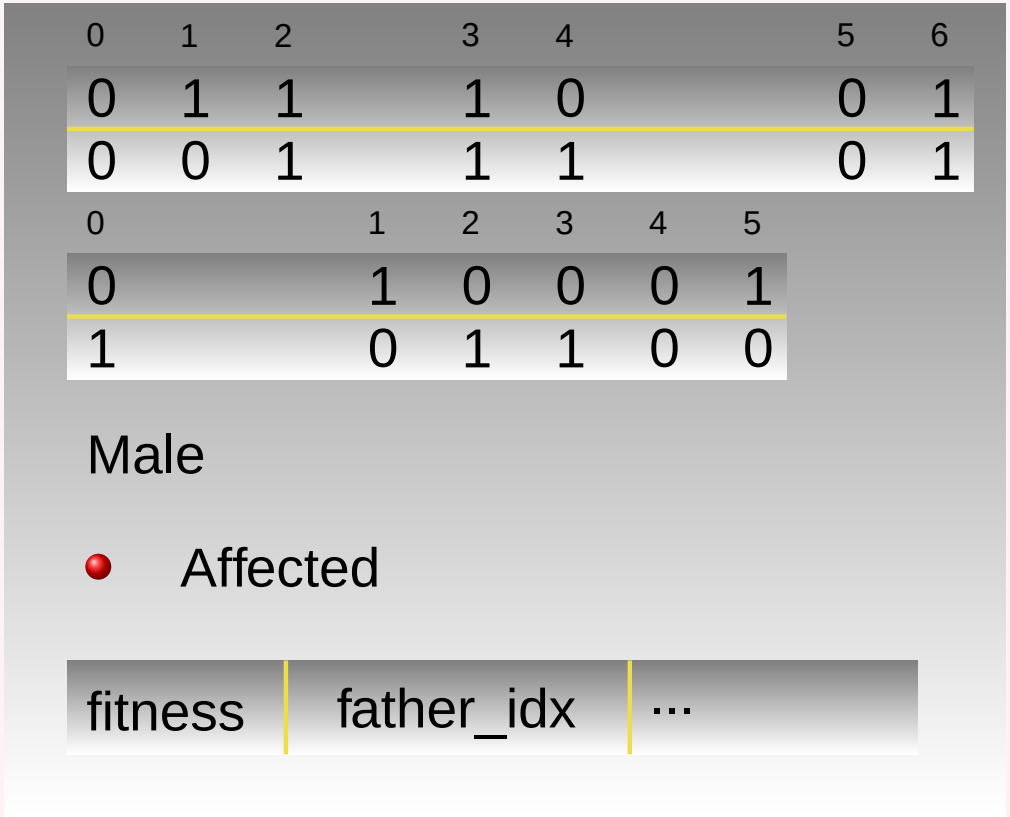

Chromosome 0

Structure of individuals

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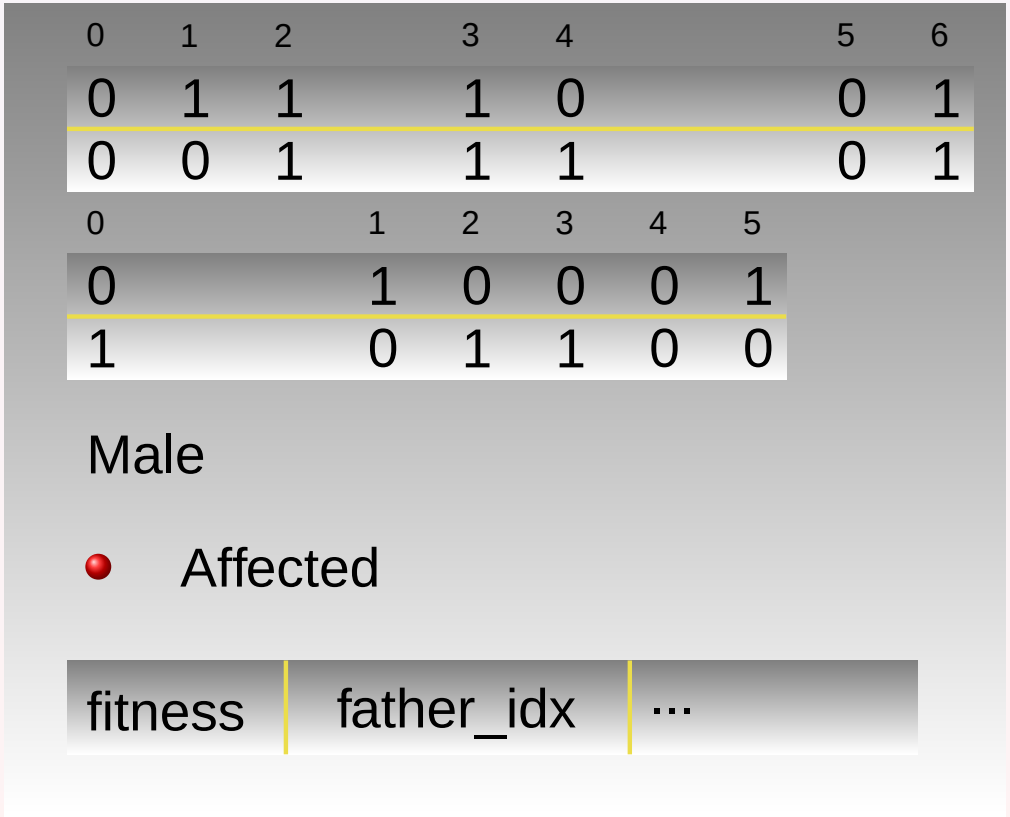

Chromosome 0

Chromosome 1

Structure of individuals

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- Features of simuPOP
- Availability

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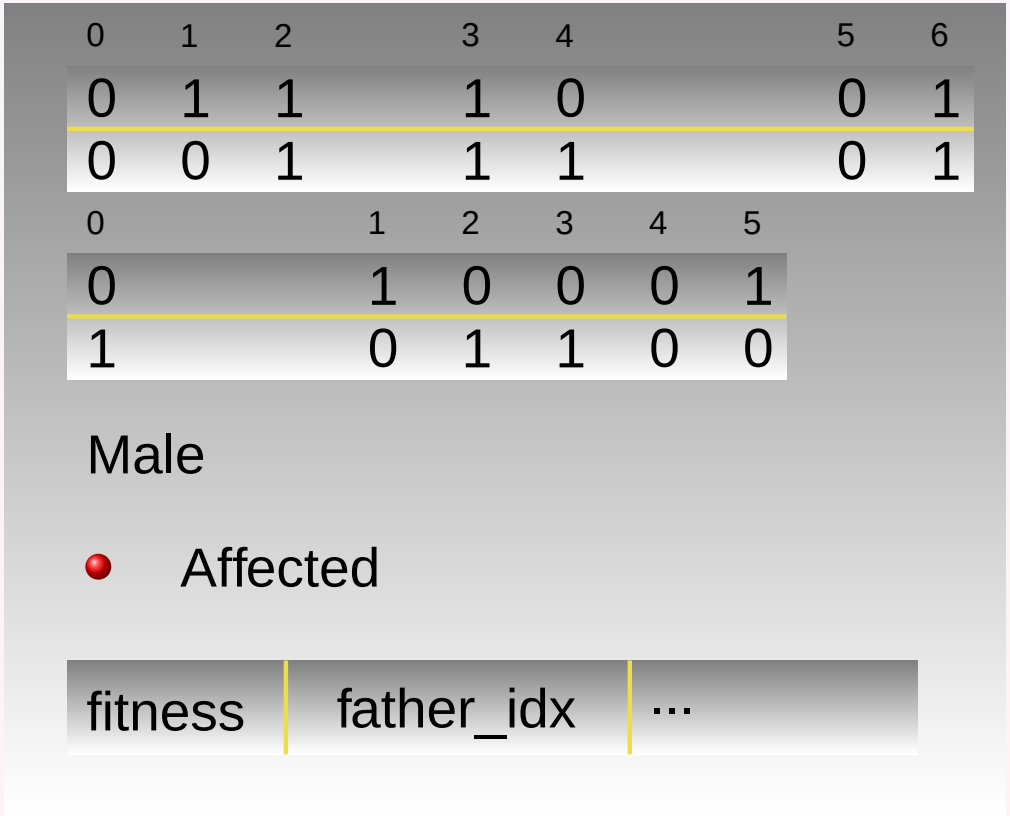
Bundled Scripts

Assume ploidy = 2, maxAllele = 1



Structure of individuals

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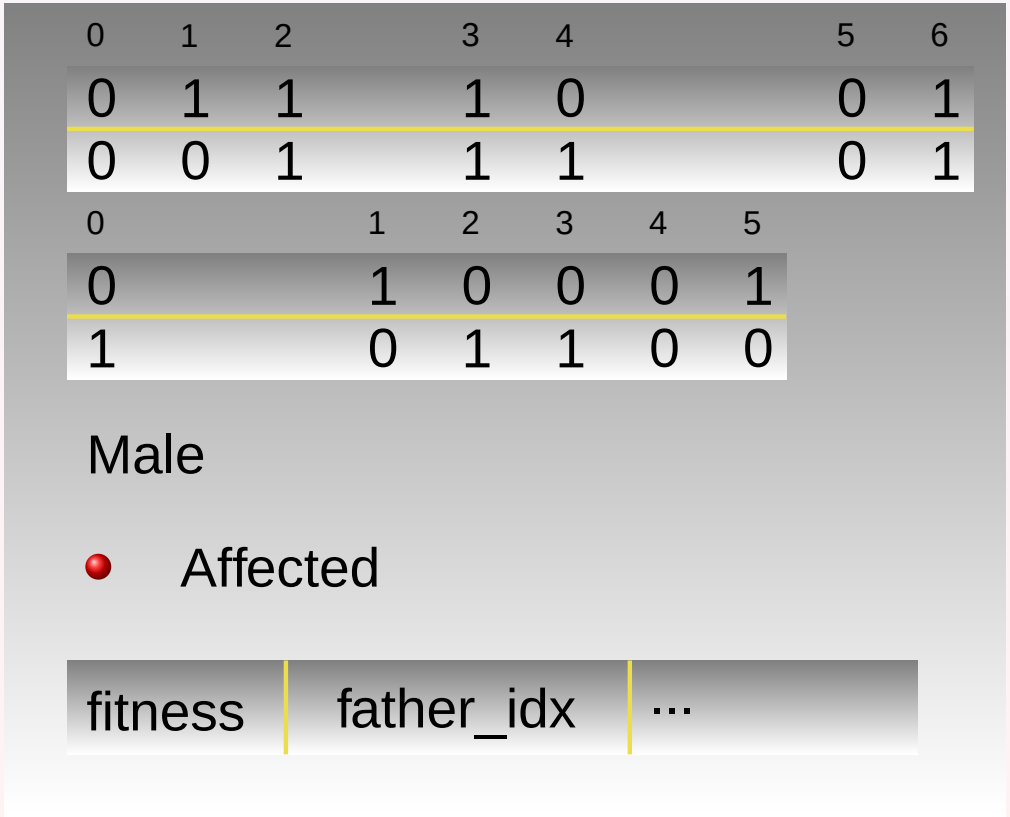

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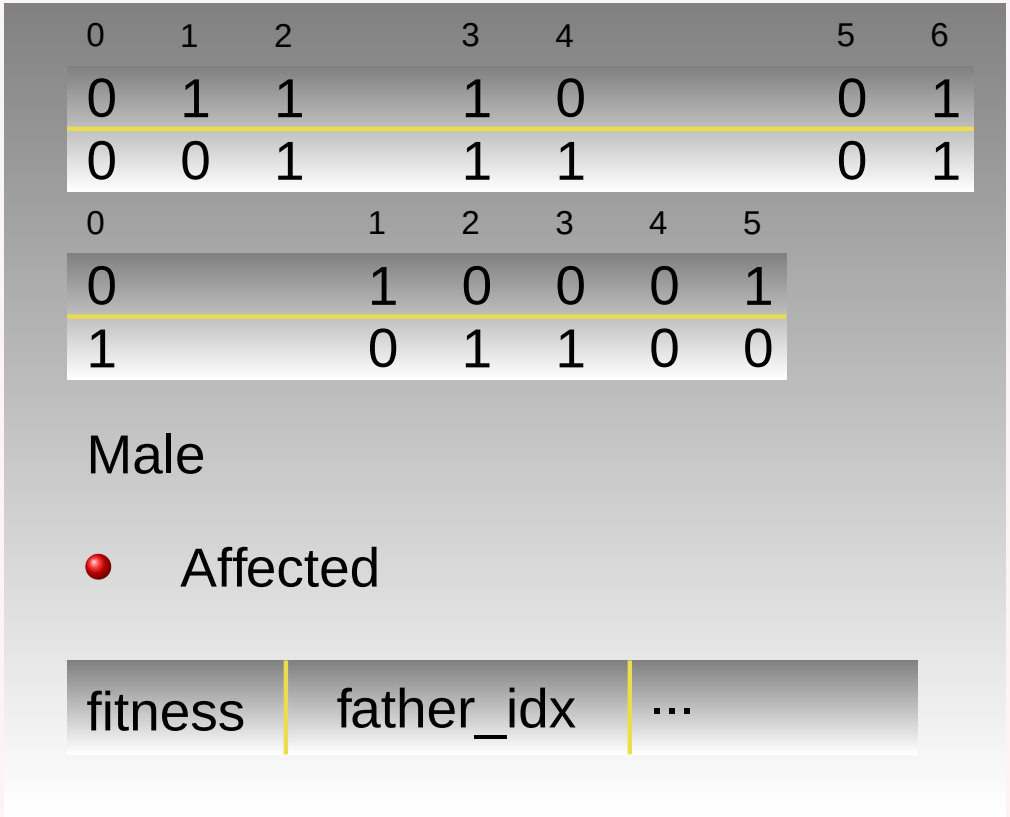

Structure of populations

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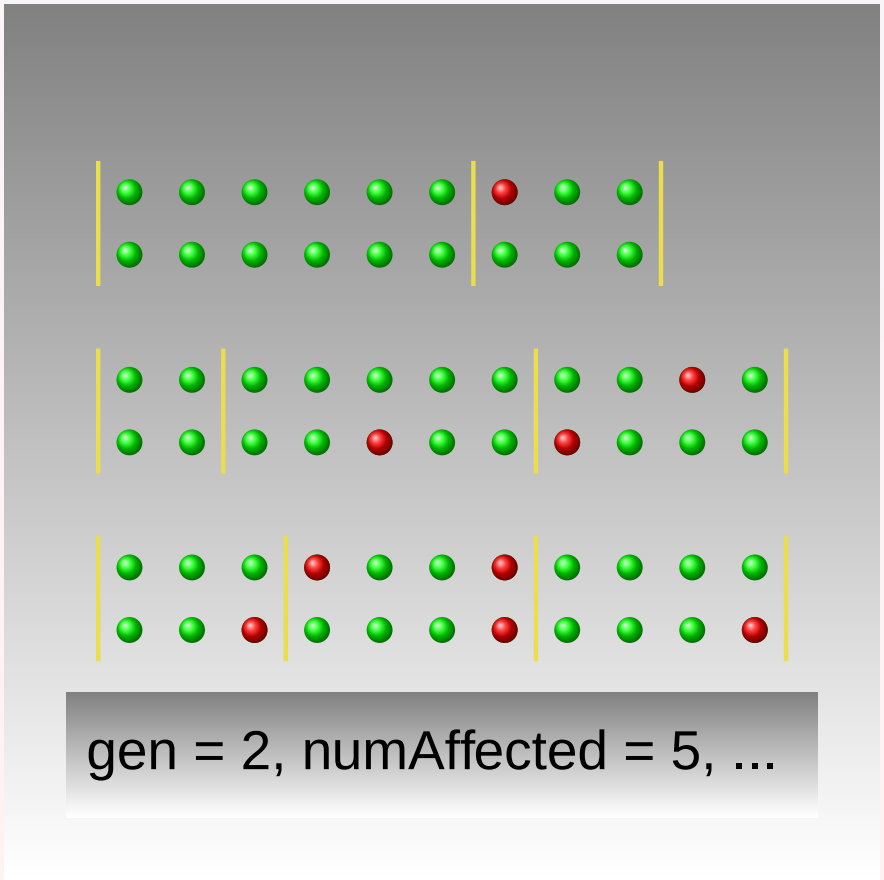
Bundled Scripts

- Unaffected
- Affected



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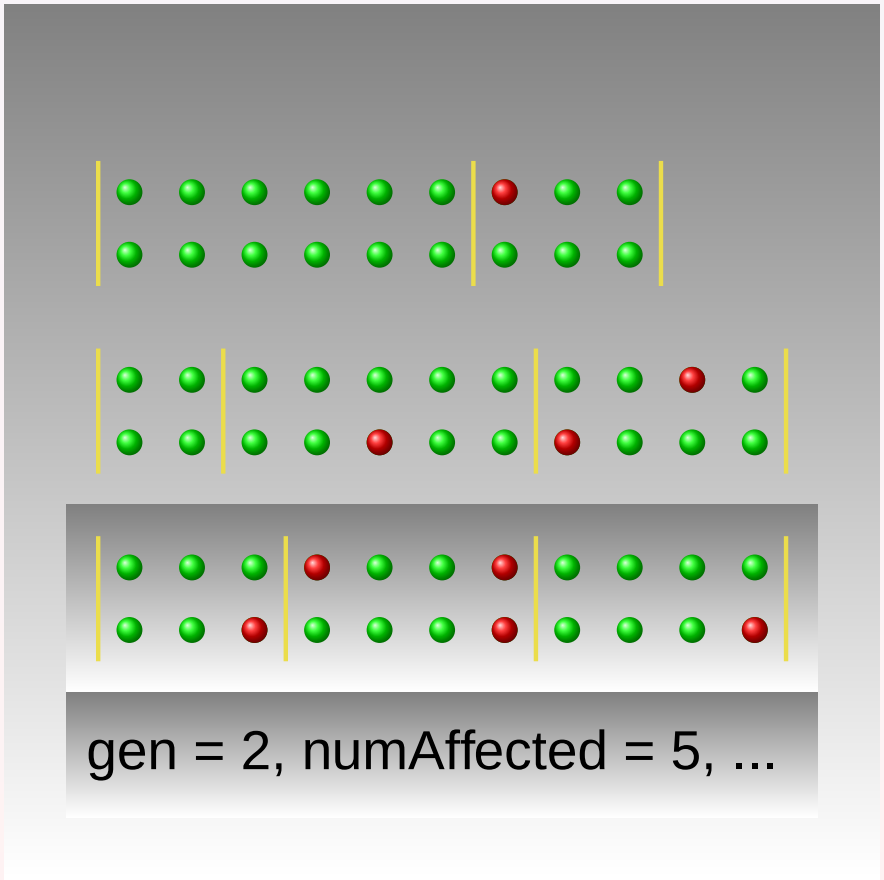

Current generation

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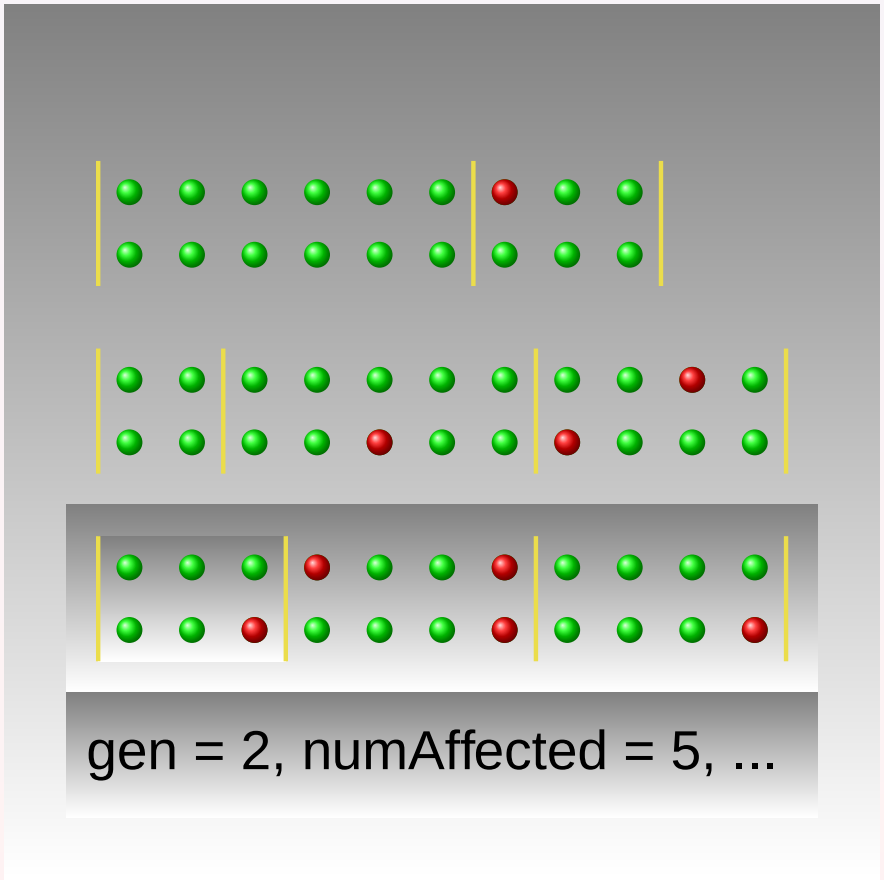

Current generation

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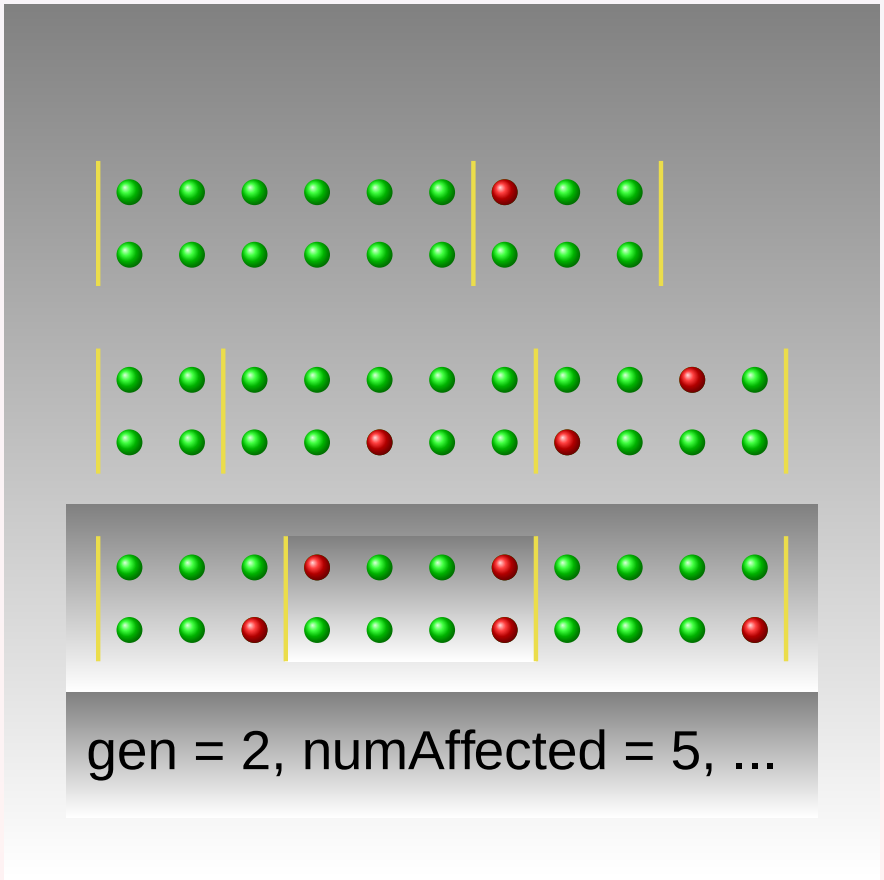

Current generation

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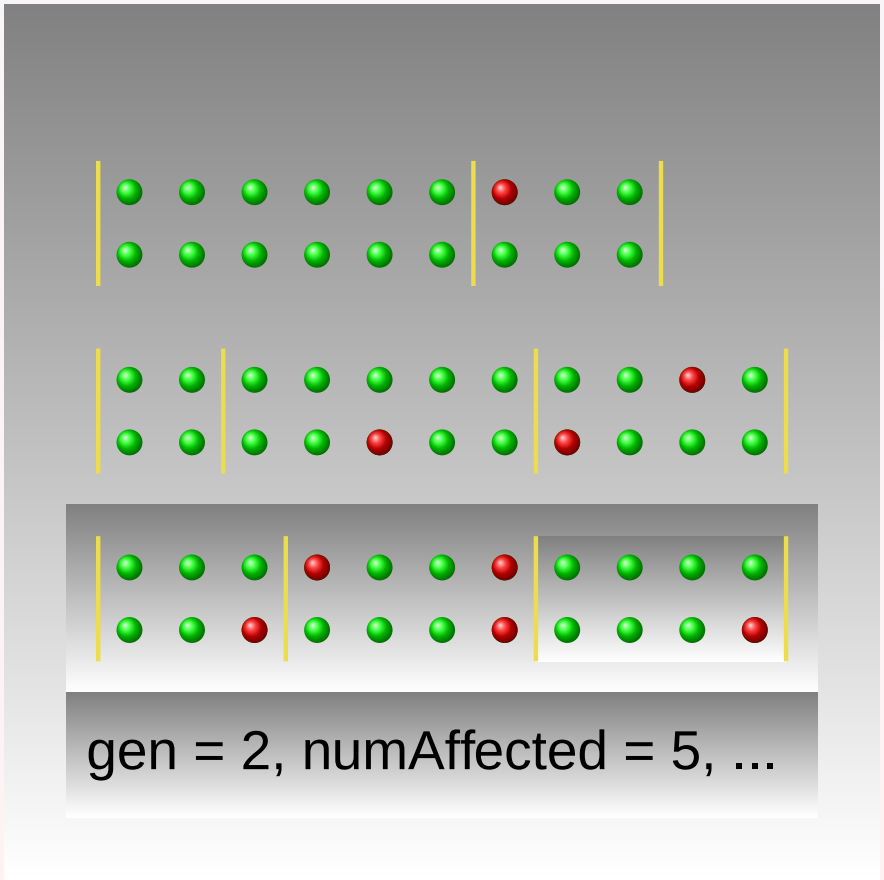

Current generation

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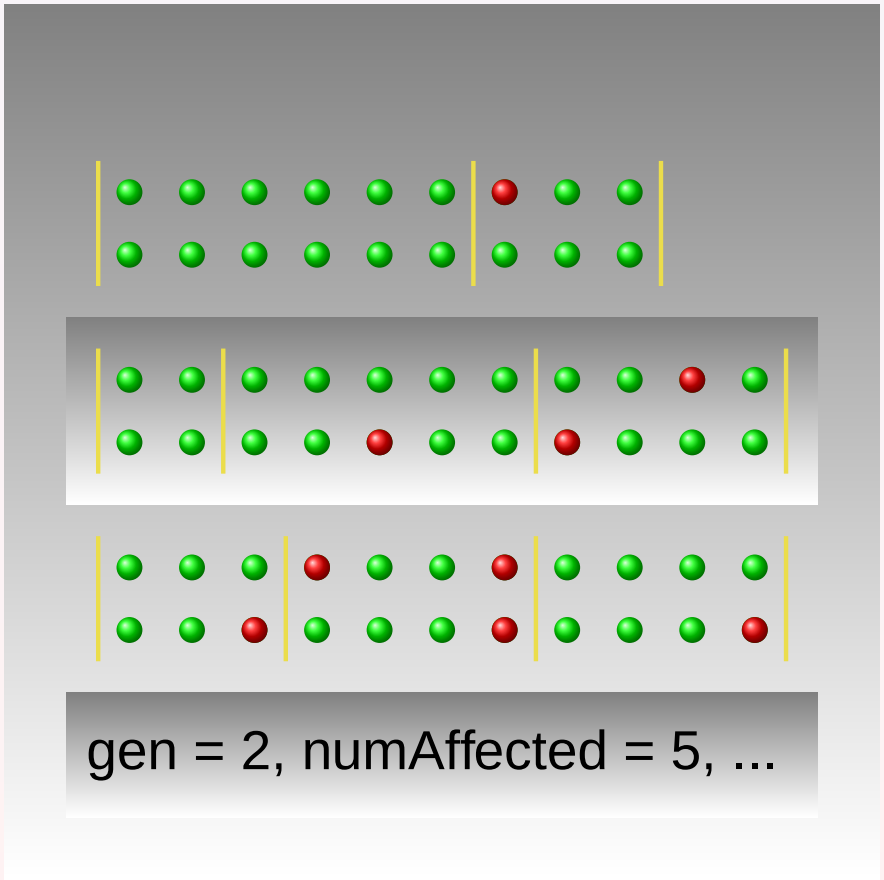

Ancestral generation 1

Current generation

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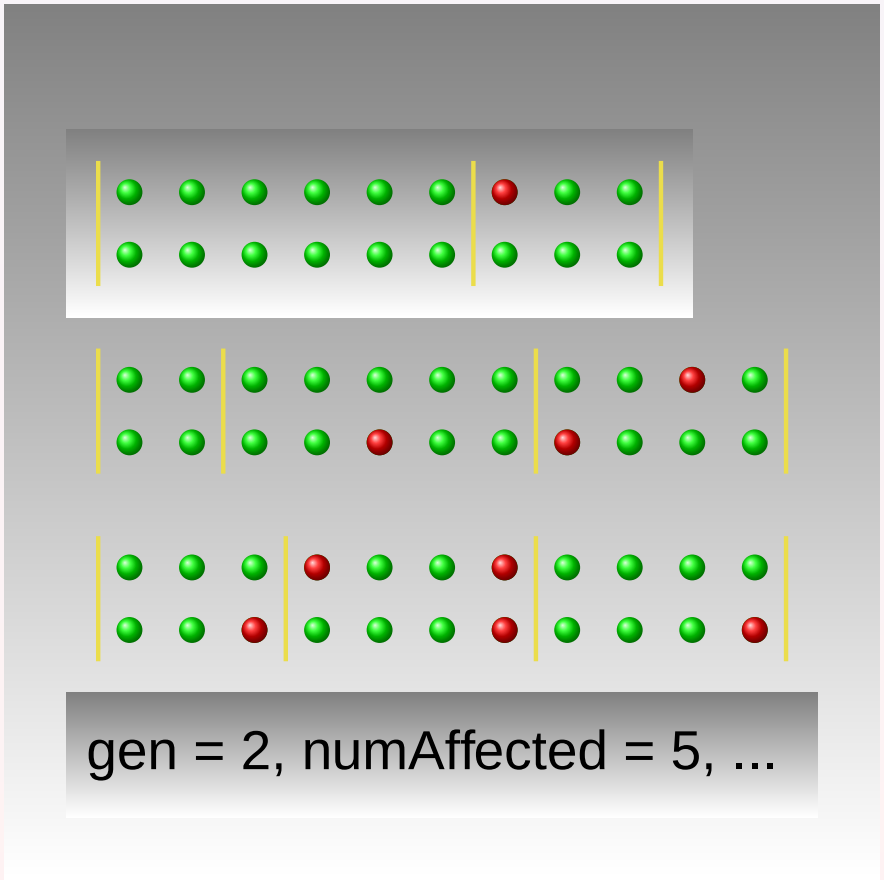
- Unaffected
- Affected



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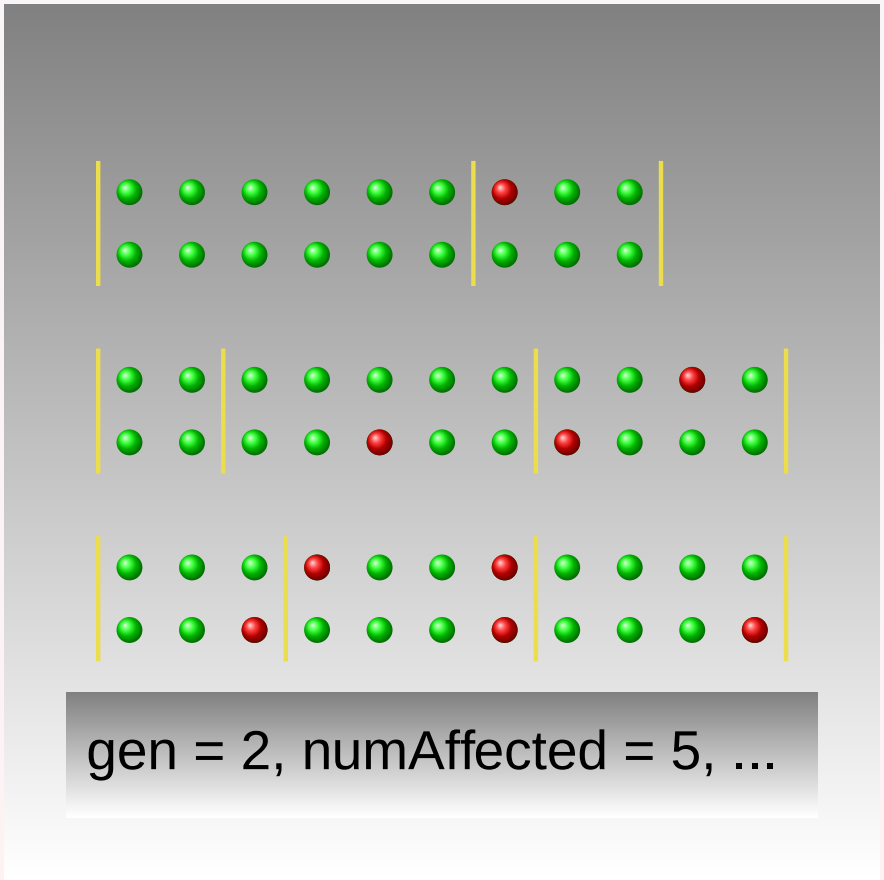

Ancestral generation 2

Ancestral generation 1

Current generation

Population variables

The evolutionary process

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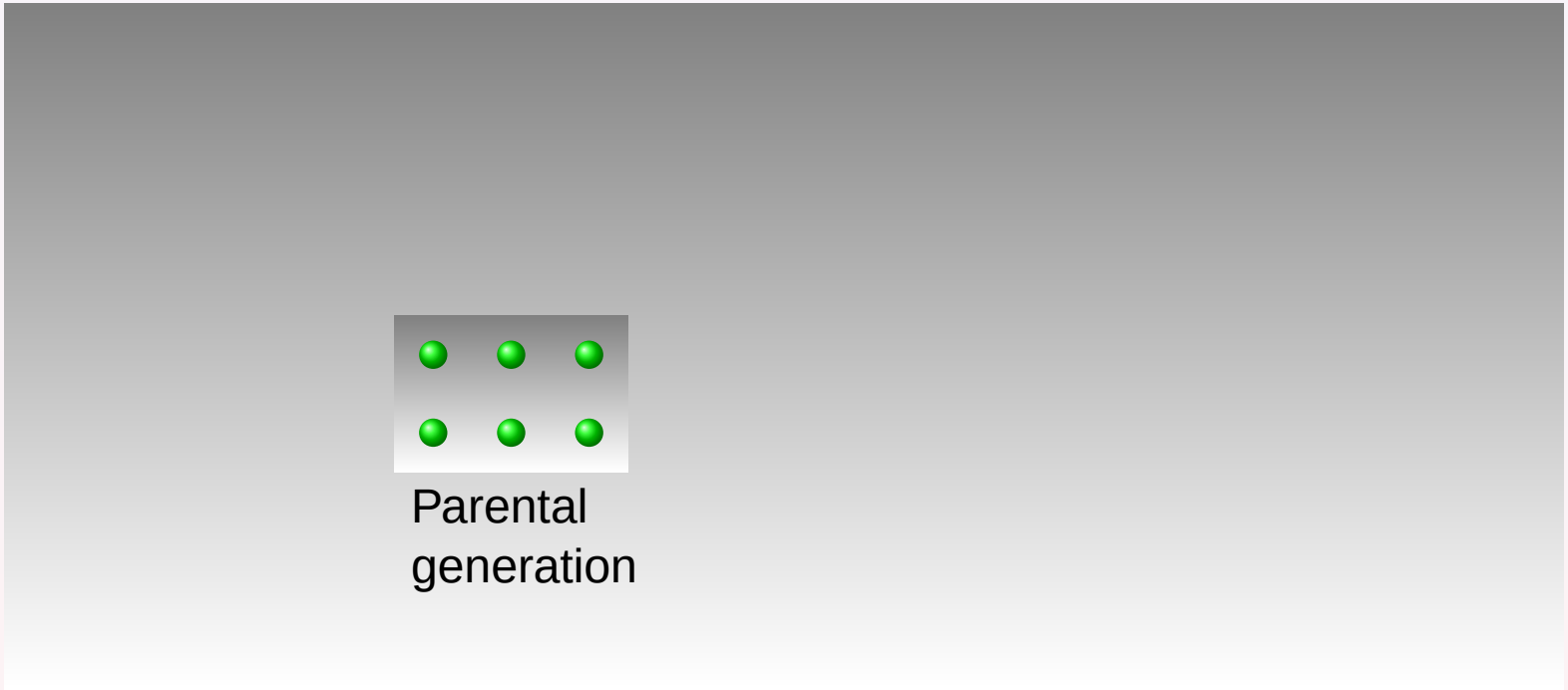

Involved simuPOP objects: population and individual, operator, mating scheme, simulator

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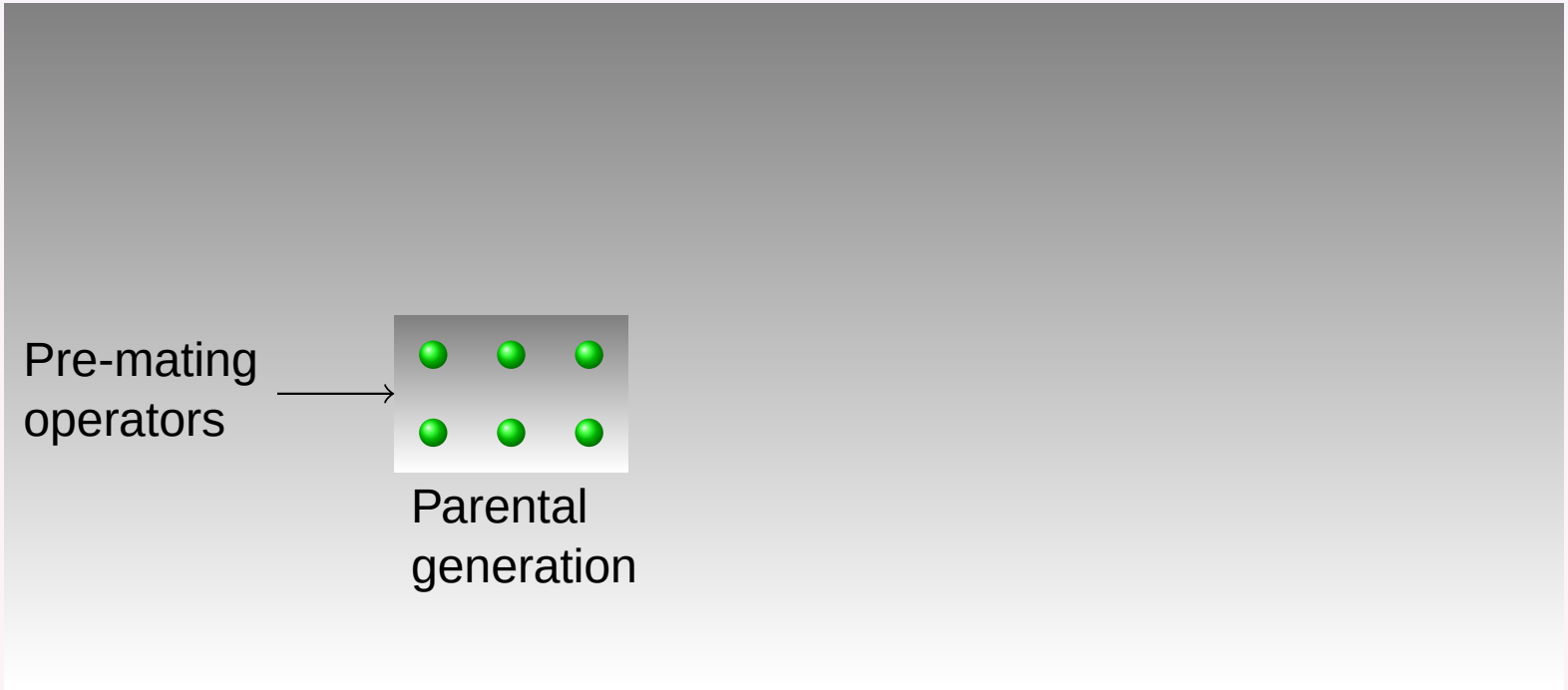

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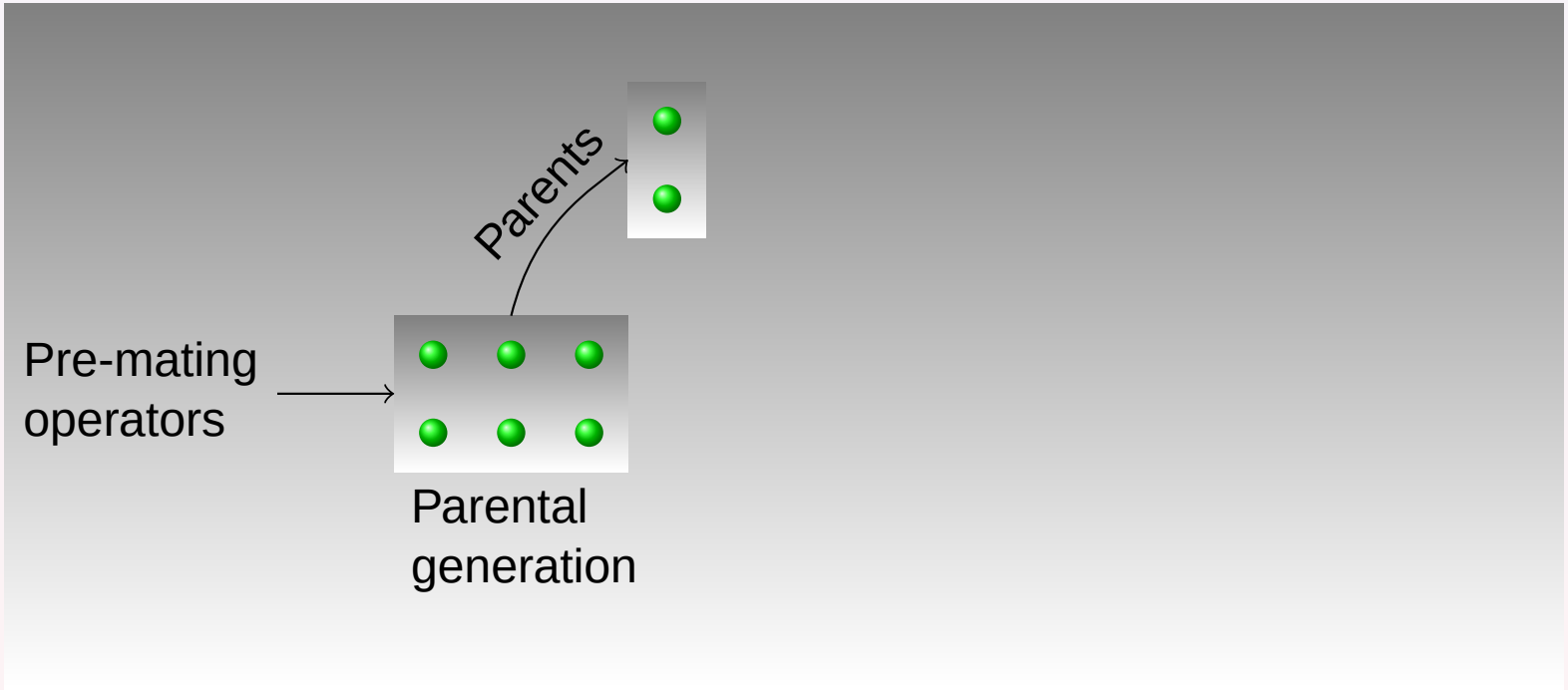

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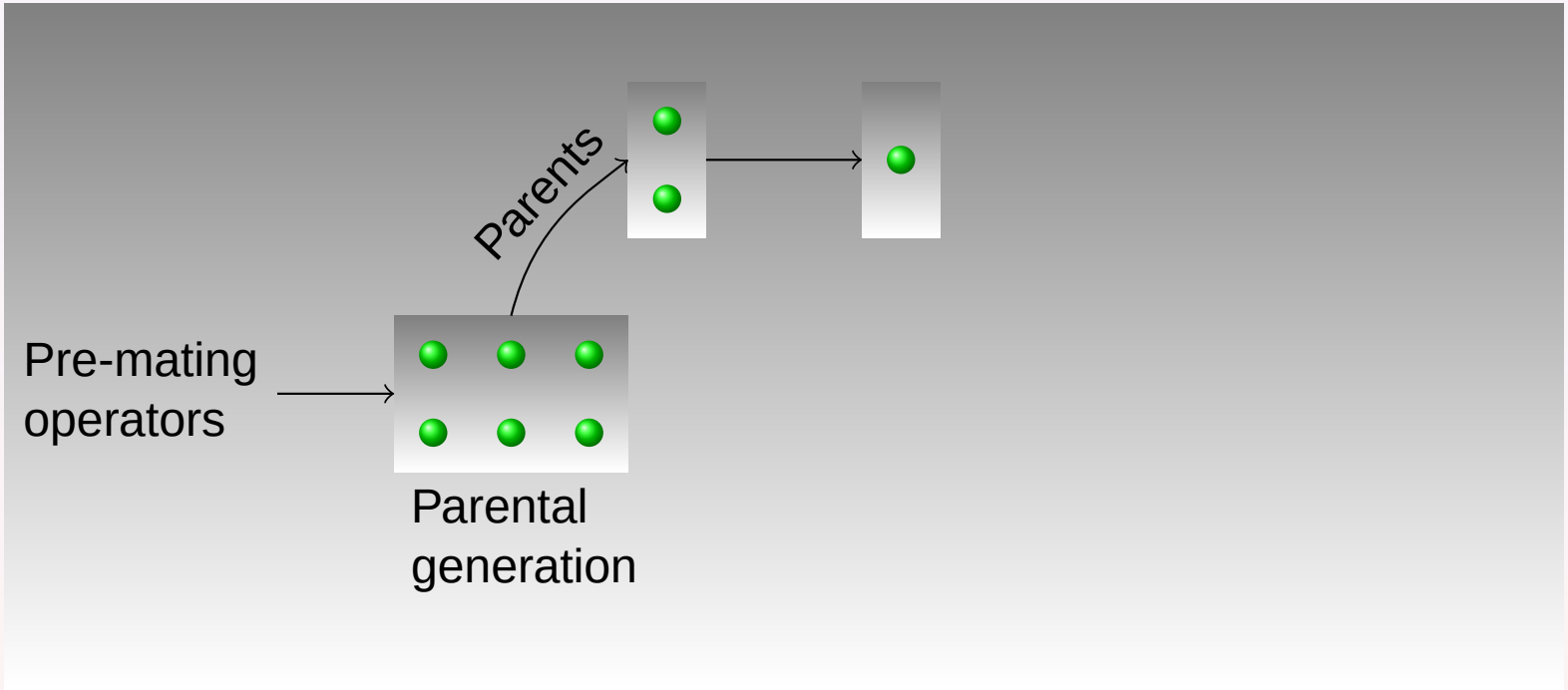

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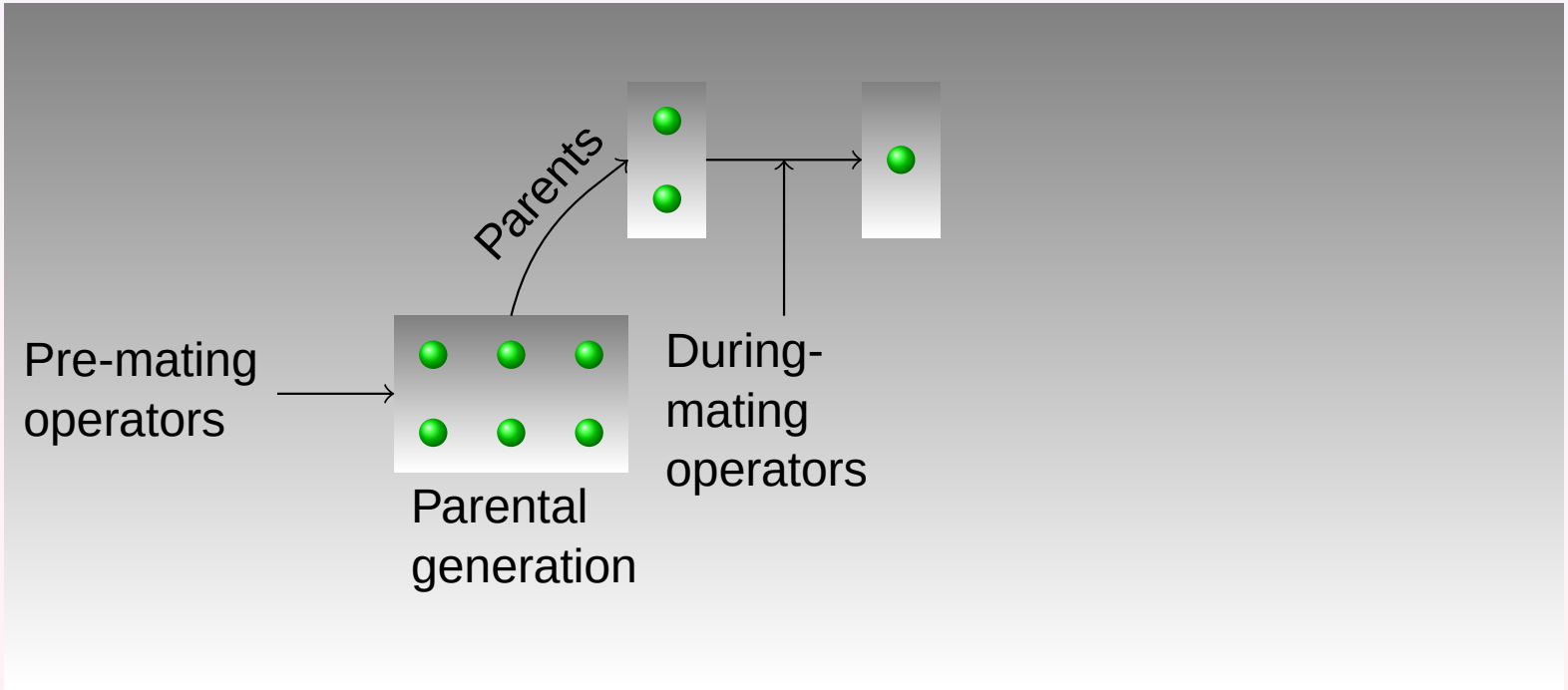

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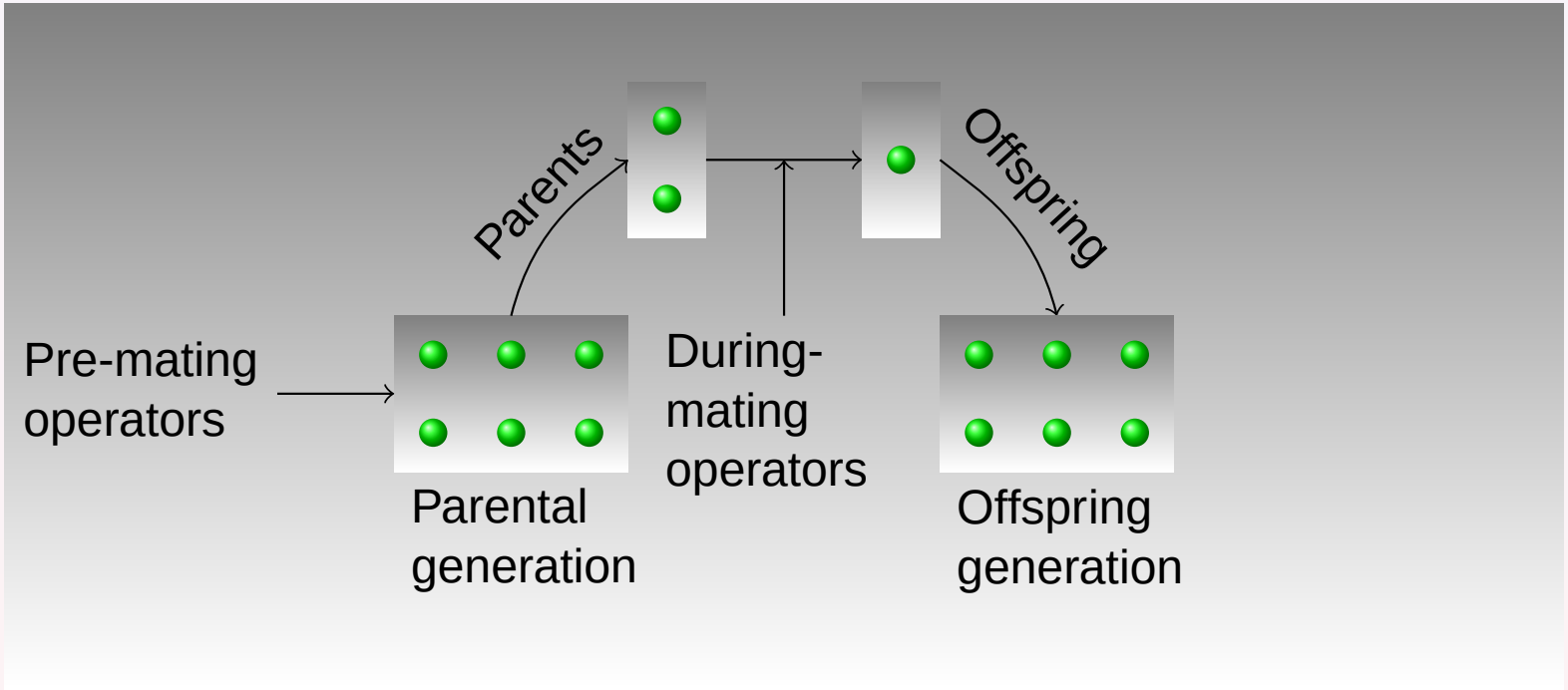

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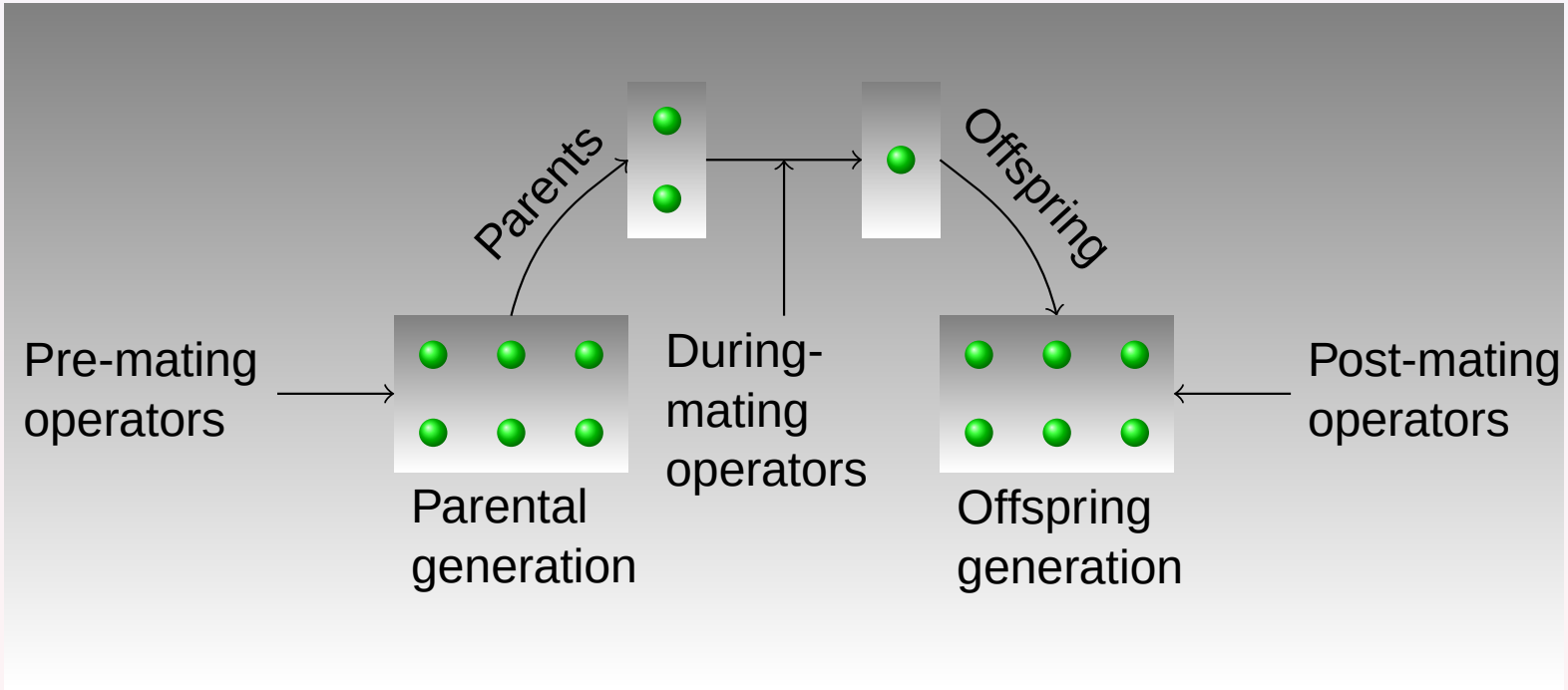

Involved simuPOP objects: population and individual, operator, mating scheme, simulator

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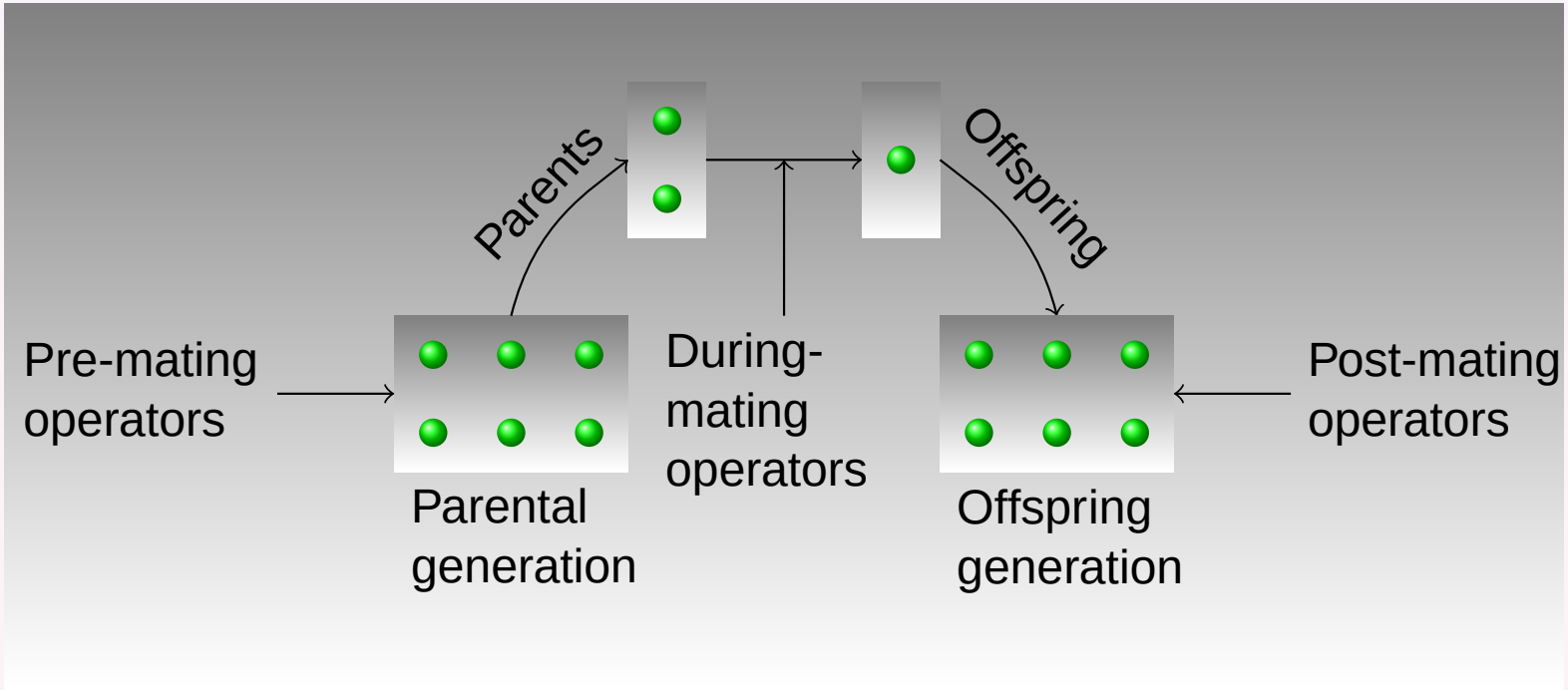

Involved simuPOP objects: population and individual, operator, mating scheme, simulator

What distinguishes simuPOP from others

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scripting simuPOP is provided as a set of Python modules, and is therefore backed by a full-blown object-oriented programming language.

flexibility simuPOP does not impose any limit on the size of genome, population, demographic model, etc. Using a large number of standard and hybrid (Python-assisted) operators, users can simulate almost arbitrarily complex evolutionary processes.

integration Owing to the 'glue language' nature of Python, it is easy to integrate simuPOP with other languages and programs.

I like it, but, oohm, why Python??

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Bundled Scripts

- The core of simuPOP is written in C++ for efficiency
- Python is the glue language, a wrapper of the core
- Python is used to write simuPOP extensions (user interface etc)
- Python is used to provide user-defined behaviors during evolution (Python operators)

Do I have to write a script?

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simuPOP can be used in two ways:

- You should learn how to write simuPOP scripts if you
  - need a particular type of simulation for you own research, and
  - know exactly what you want to do
- You can use existing simuPOP scripts without knowing simuPOP if
  - you need to use an existing simulation scenario to simulate samples or populations
  - this scenario is implemented in simuPOP

Availability

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- simuPOP website: `http://simupop.sourceforge.net`
- Mailing list: `simupop-list@lists.sourceforge.net`
- License: GPL 2.0
- Platforms: all OS on which Python is available
- Monthly release, currently at 0.7.10
- Documentation: *simuPOP User's Guide* and *simuPOP Reference Manual*

Outline

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```
>>> from simuPOP import *
>>> simu = simulator(
...     population(size=1000, ploidy=2, loci=[2]),
...     randomMating(),
...     rep = 3)
>>> simu.evolve(
...     preOps = [initByValue([1,2,2,1])],
...     ops = [
...         recombinator(rate=0.1),
...         stat(LD=[0,1]),
...         pyEval(r"'%3d    ' % gen", rep=0, step=10),
...         pyEval(r"'%f     ' % LD[0][1]", step=10),
...         pyEval(r"'\n'", rep=REP_LAST, step=10)
...     ],
...     end=100
... )
```

Loading simuPOP module

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Import the default simuPOP module

population

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```
>>> from simuPOP import *
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...     rep = 3)
```

Create a `population` of 1000 `diploid` individuals, each having two `loci` on the first chromosome

simulator and mating scheme

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```
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...     rep = 3)
```

Create a `simulator` that has one replicate of this population, and a random mating scheme

Operators!

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...     ],
...     end=100
... )
```

`initByValue` is applied before evolution

Operators!

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...     ],
...     end=100
... )
```

`recombinator` is applied at every generation when an offspring is produced

Operators!

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...         pyEval(r"'%f     ' % LD[0][1]", step=10),
...         pyEval(r"'\n'", rep=REP_LAST, step=10)
...     ],
...     end=100
... )
```

`stat` is applied to the offspring generation at every generation

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...         pyEval(r"'%f    ' % LD[0][1]", step=10),
...         pyEval(r"'\n'", rep=REP_LAST, step=10)
...     ],
...     end=100
... )
```

`pyEval` is applied every 10 generations

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...         pyEval(r"'%f     ' % LD[0][1]", step=10),
...         pyEval(r"'\n'", rep=REP_LAST, step=10)
...     ],
...     end=100
... )
```

Output of the example

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```
  0    0.198245    0.194438    0.200940
 10    0.070979    0.057269    0.063011
 20    0.022691    0.022680    0.026061
 30    0.016645    0.008160    0.016585
 40    0.006175    0.012946    0.015404
 50    0.004759    0.004210    0.004058
 60    0.003378    0.010928    0.009723
 70    0.001021    0.015047    0.017137
 80    0.002260    0.010912    0.022643
 90    0.006783    0.004700    0.007016
100    0.012960    0.015493    0.015612
```

Use R to plot

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```
>>> from simuPOP import *
>>> from simuRPy import *
>>> simu = simulator(
...     population(size=1000, ploidy=2, loci=[2]),
...     randomMating(),
...     rep = 3)
>>> simu.evolve(
...     preOps = [initByValue([1,2,2,1])],
...     ops = [
...         recombinator(rate=0.1),
...         stat(LD=[0,1]),
...         varPlotter('LD[0][1]', numRep=3, step=10,
...             saveAs='ld', ylim=[0,.25],
...             lty=range(1, 4), col=range(2, 5),
...             xlab='generation', ylab='D',
...             title='LD Decay'),
...     ],
...     end=100
... )
True
>>>
```

Evolve!

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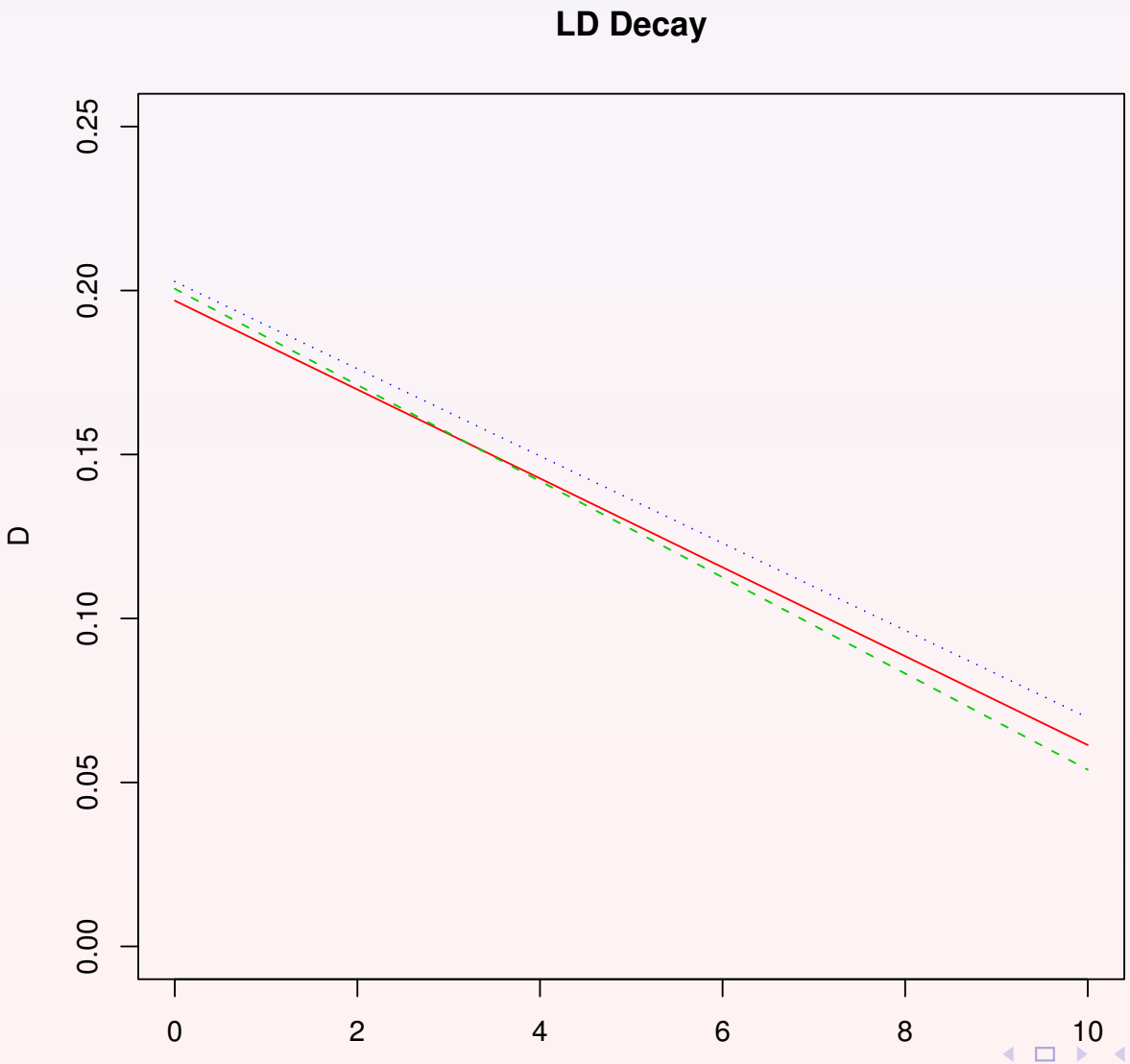
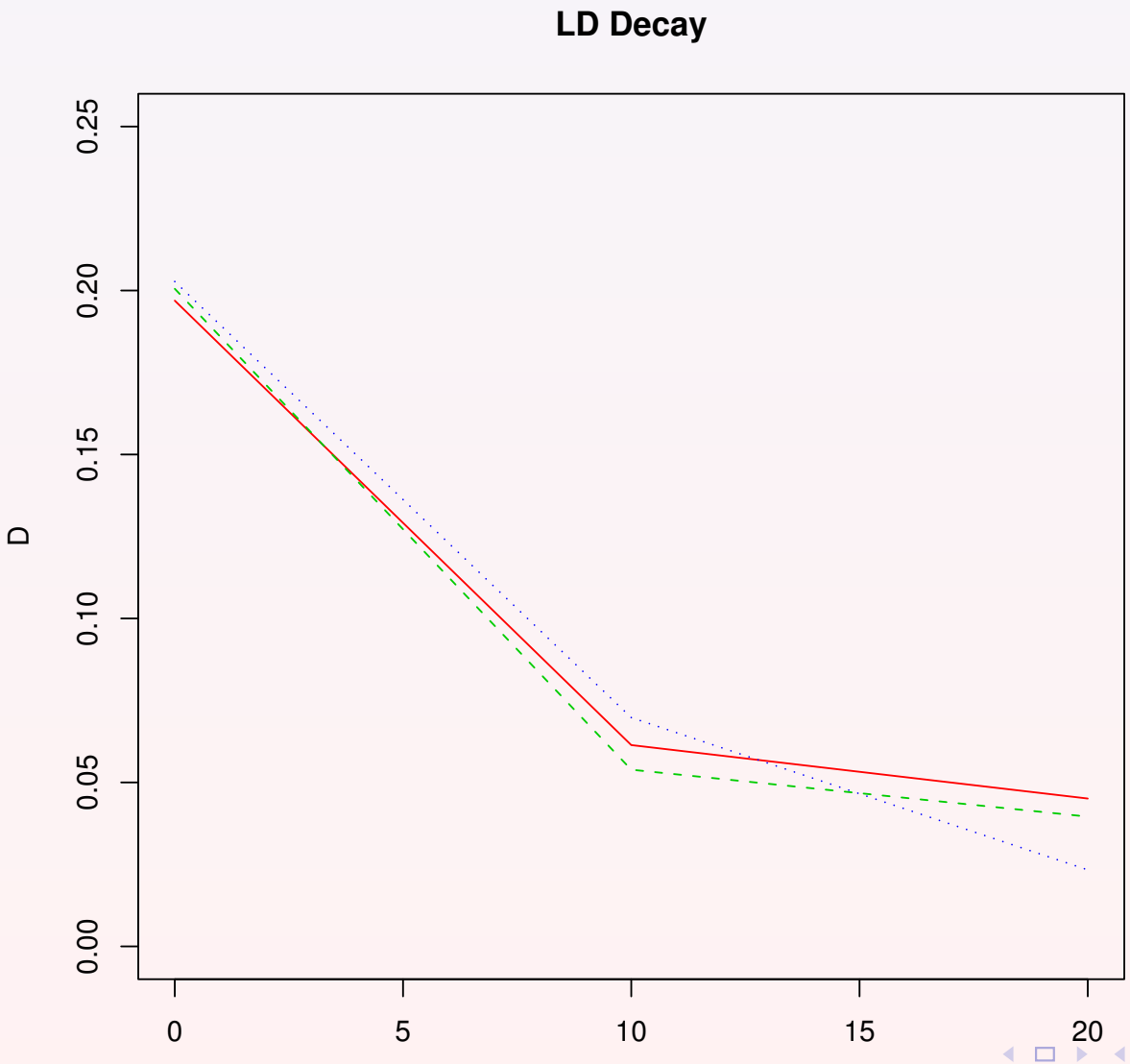


- Update at every 10 generations
- LD=0.25 before generation 0
- LD is calculated at the end of each generation

Evolve!



- Update at every 10 generations
- LD=0.25 before generation 0
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Evolve!

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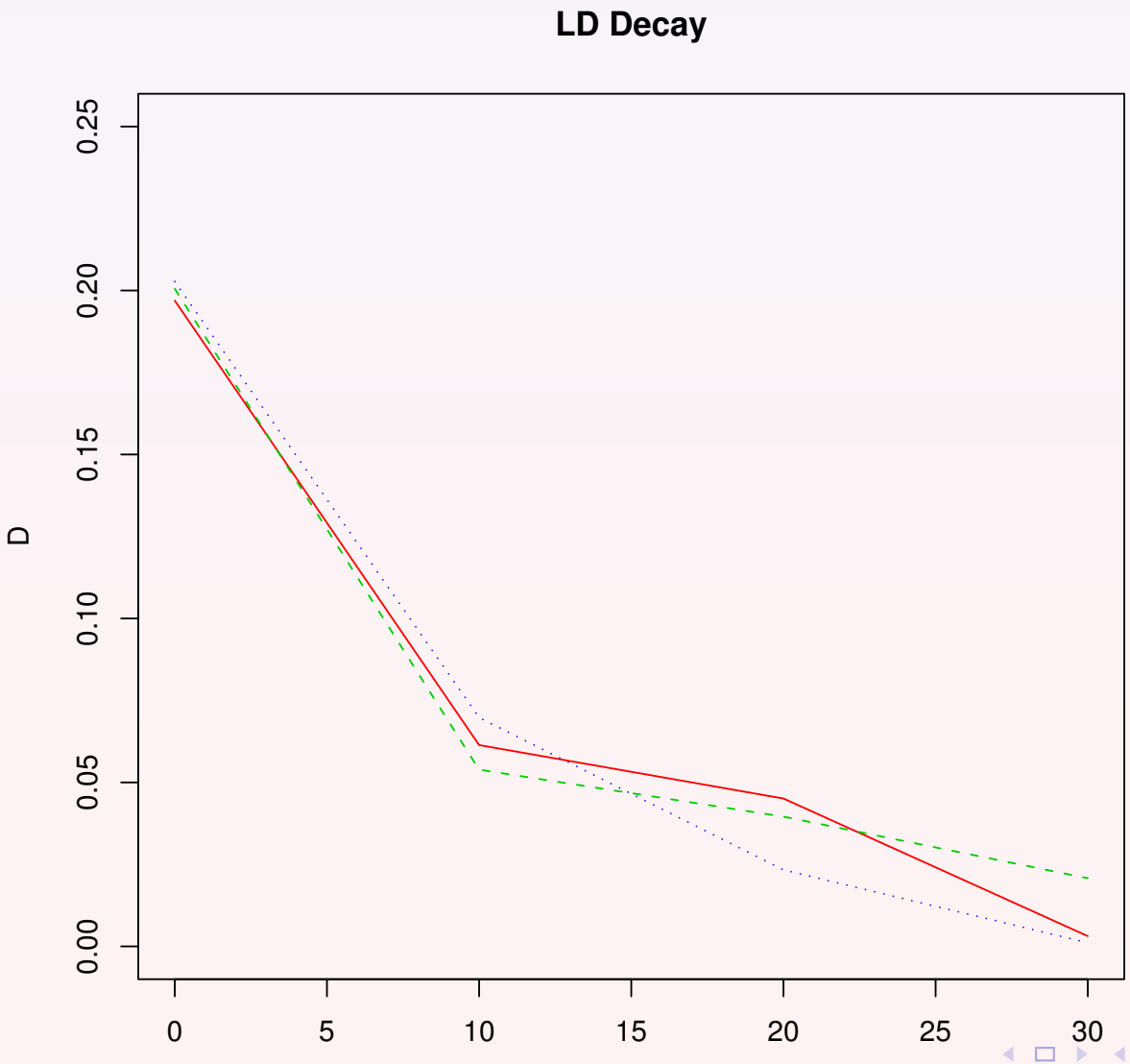

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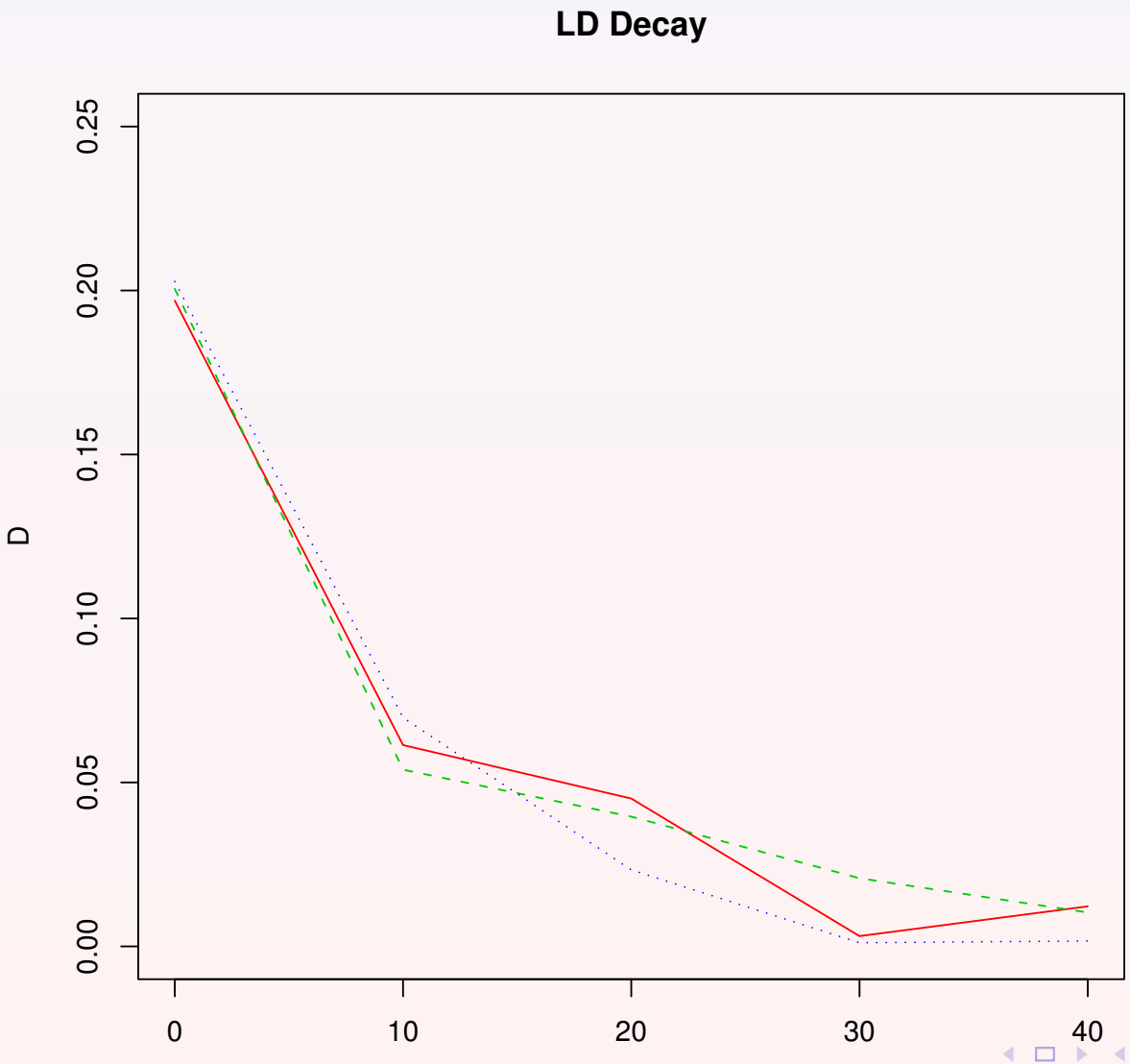

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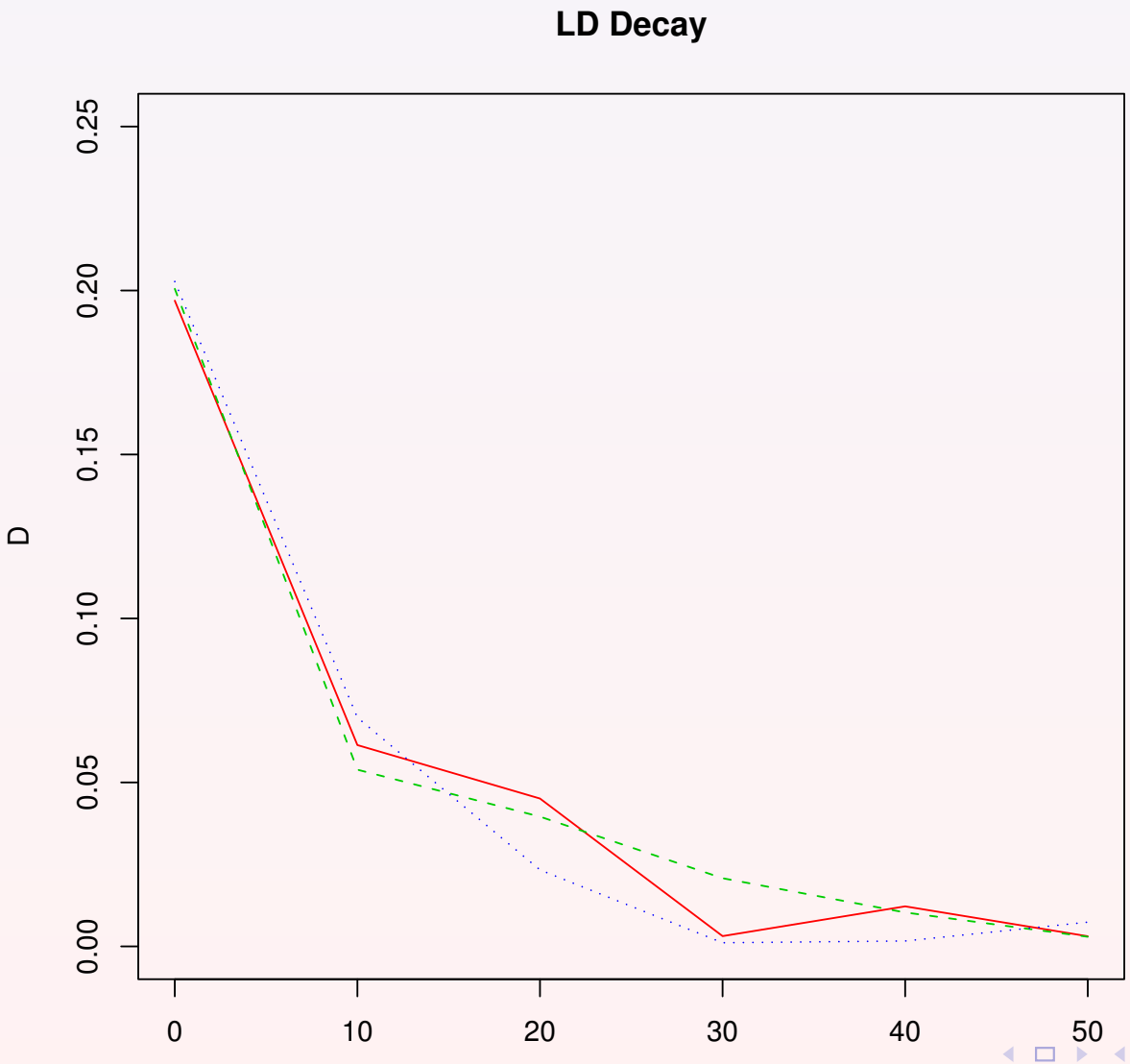

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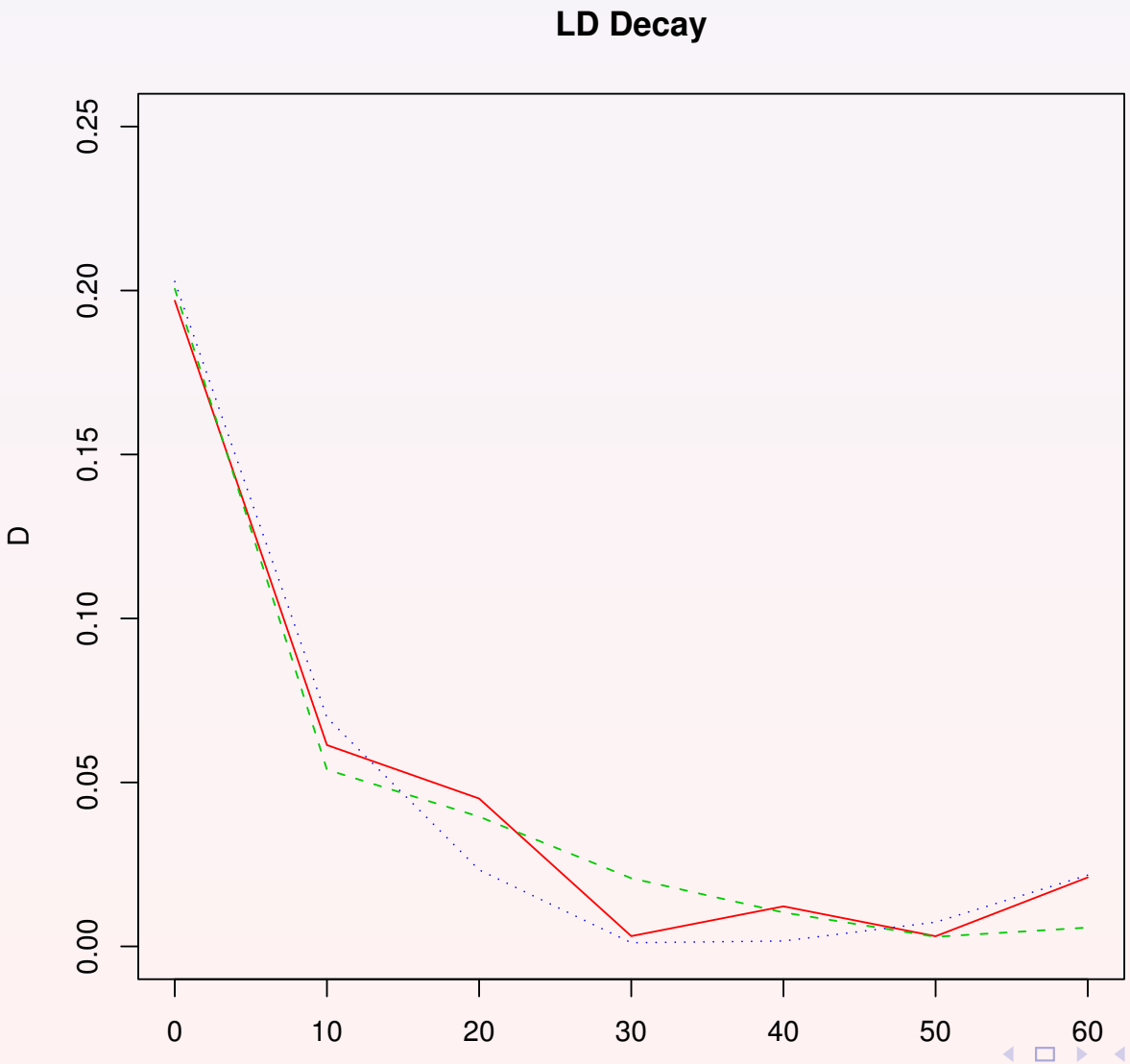

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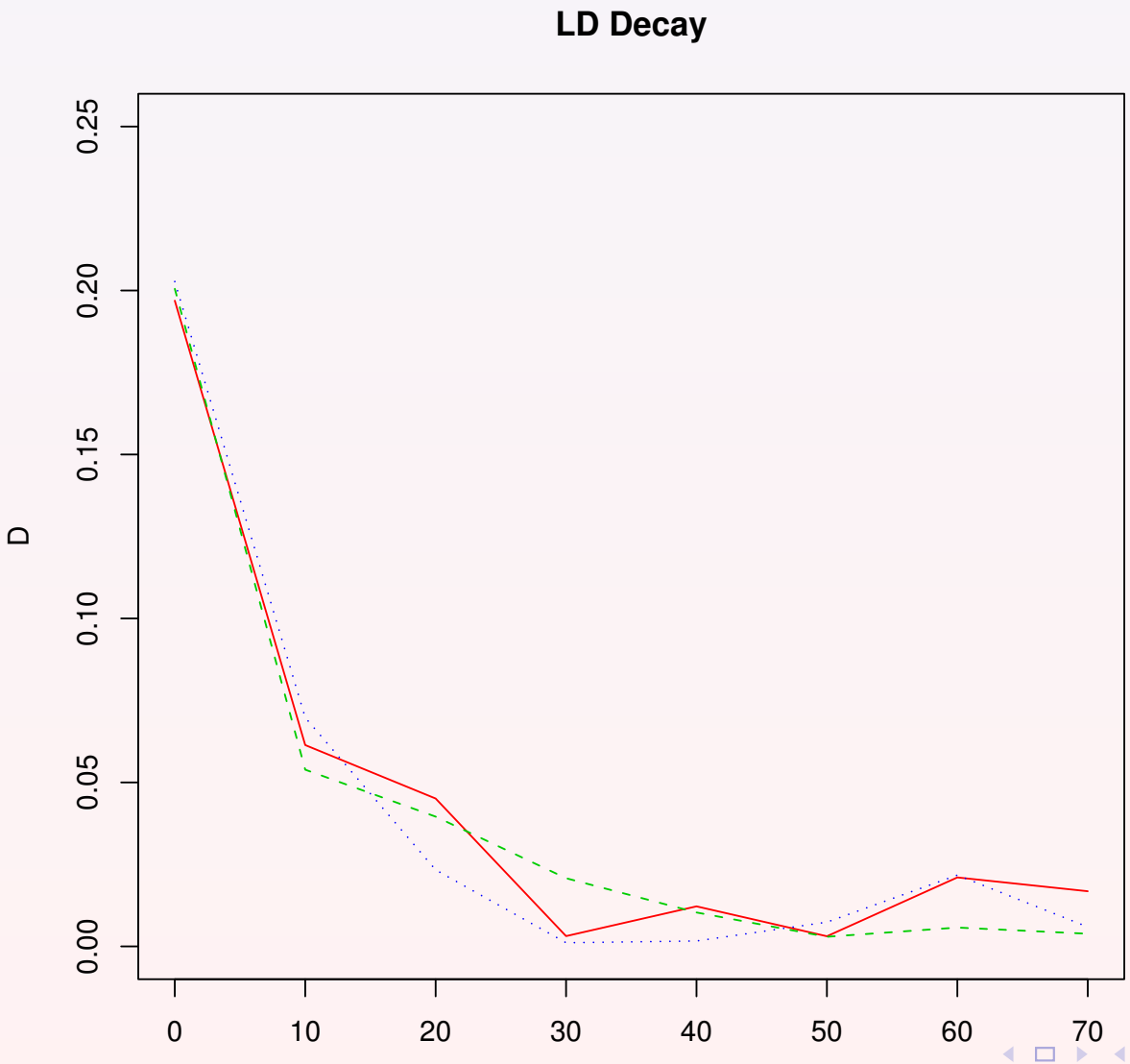
Evolve!



- Update at every 10 generations
- LD=0.25 before generation 0
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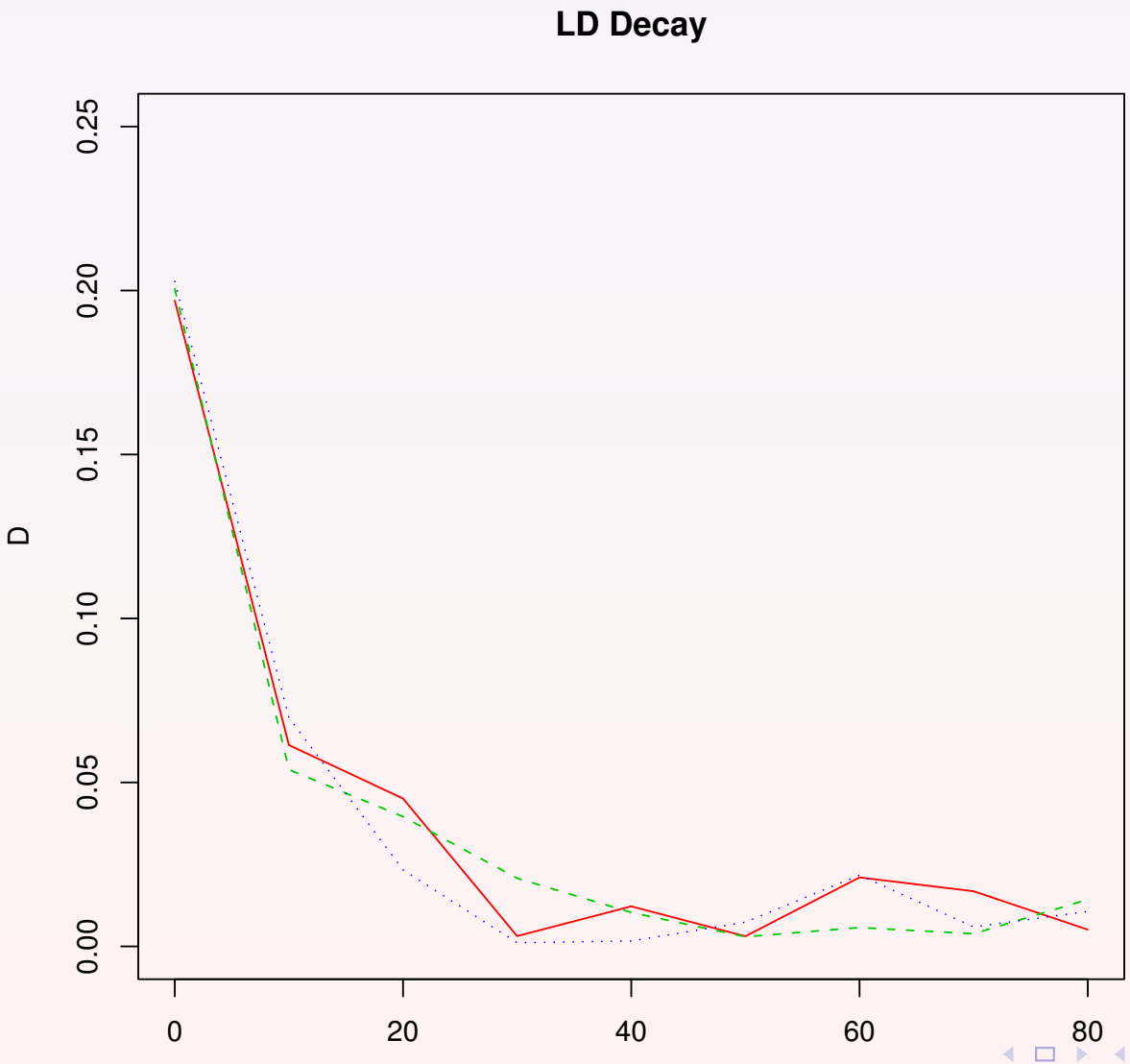

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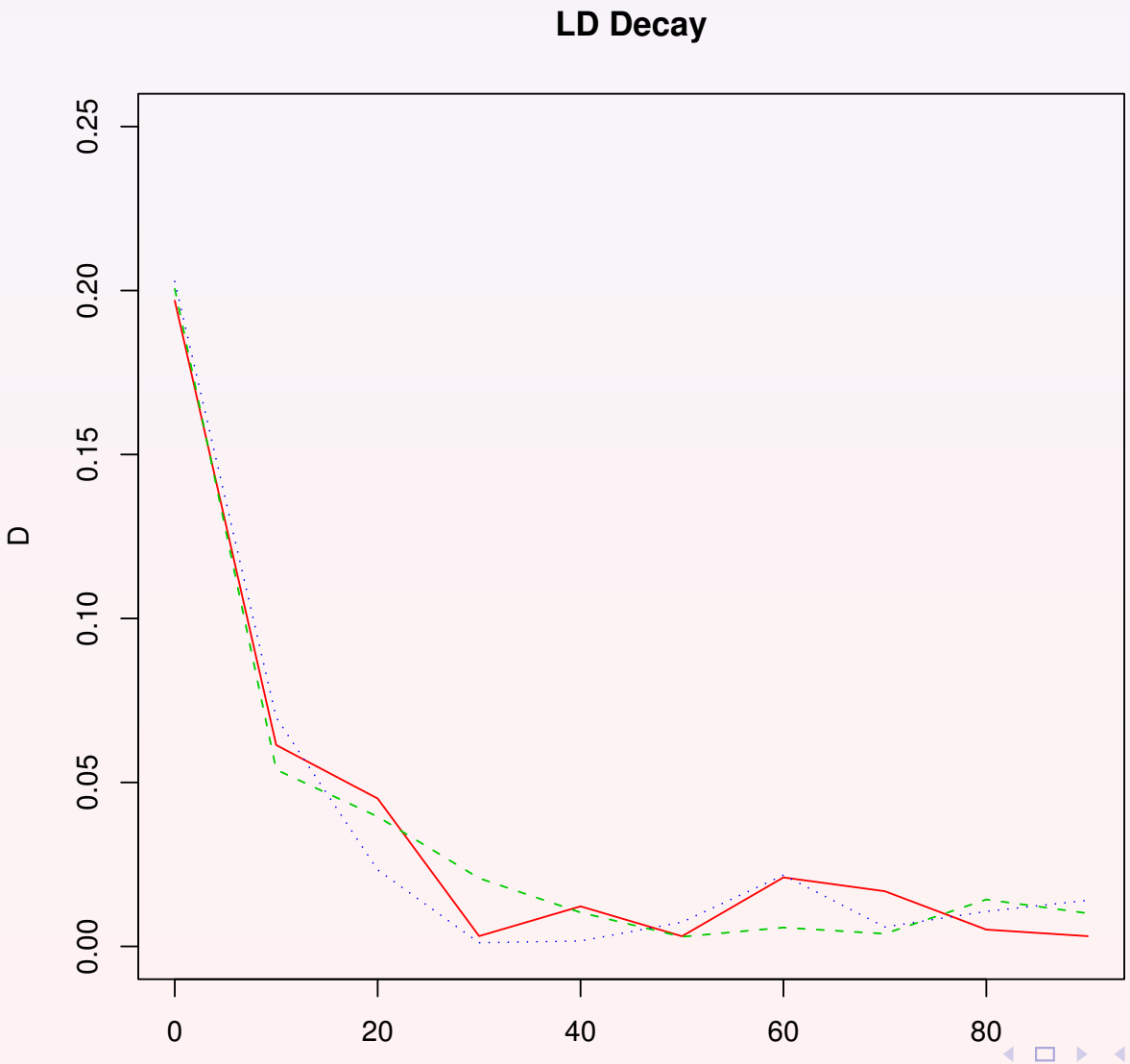

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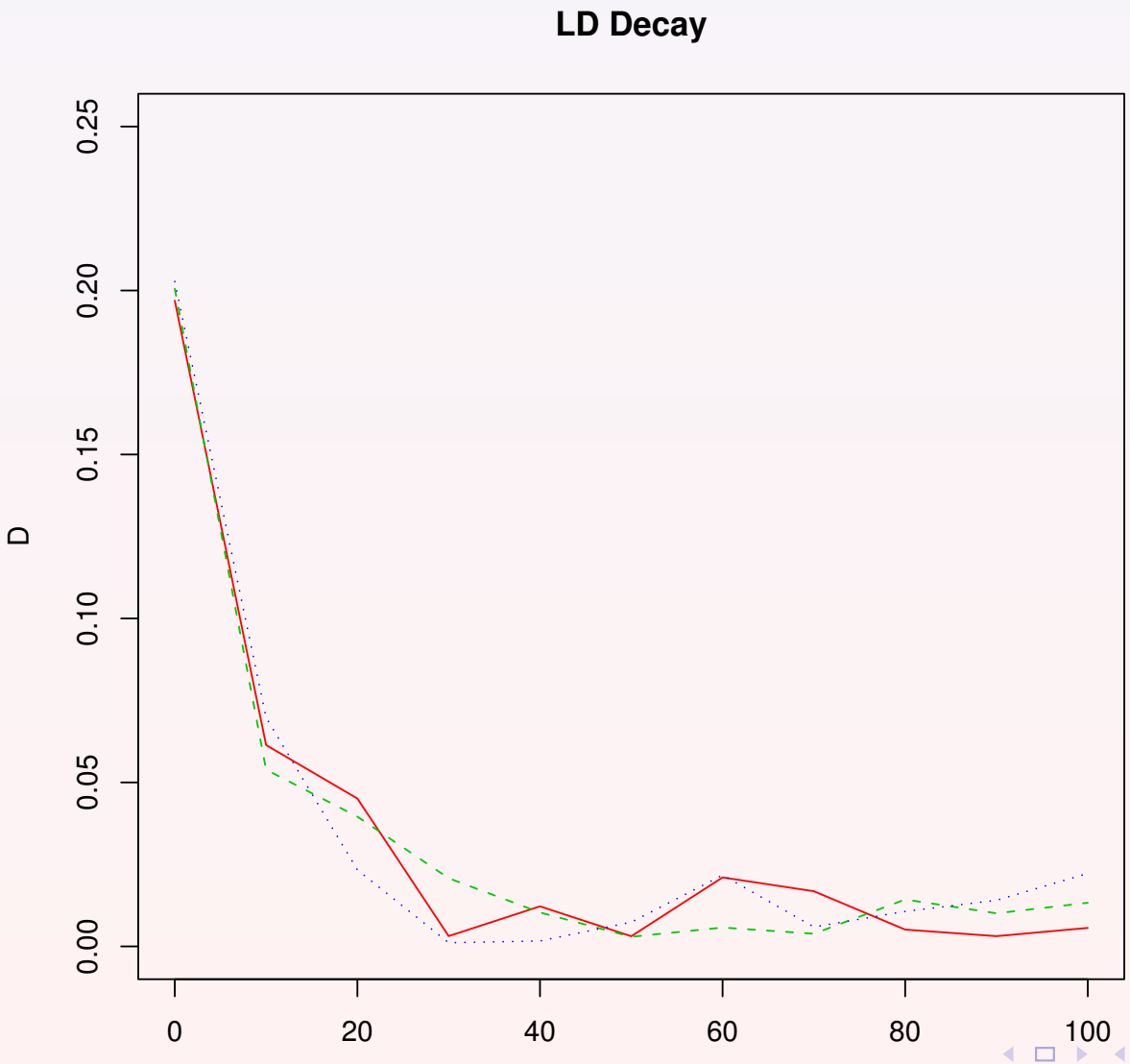

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- LD=0.25 before generation 0
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```
>>> def lin_inc(gen, oldsize=[]):
...     return [10+gen]*5
...
>>> simu = simulator(
...     population(subPop=[5]*5, loci=[1]),
...     randomMating(newSubPopSizeFunc=lin_inc)
... )
>>> simu.evolve(
...     ops = [
...         stat(popSize=True),
...         pyEval(r'"%d %d\n"%(gen, subPop[0]["popSize"])'),
...     ],
...     end=5
... )
0 10
1 11
2 12
3 13
4 14
5 15
True
>>>
```

Calculate statistics

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```
>>> simu = simulator(
...     population(subPop=[10000]*2, loci=[10]),
...     randomMating()
... )
>>> simu.evolve(
...     preOps = [
...         initByFreq([0.2, 0.8], subPop=[0]),
...         initByFreq([0.8, 0.2], subPop=[1]),
...     ],
...     ops = [
...         stat(LD=[[0,1], [5,6]], Fst=range(10), step=100),
...         migrator(rate=[[0, 0.01], [0, 0.02]]),
...         pyEval(r'"Gen: %4d LD: %.3f R2: %.3f Fst: %.3f\n"' \
...             ' % (gen, LD[0][1], R2[0][1], AvgFst)',
...             step=100)
...     ],
...     end=1000
... )
```

Calculate statistics (cont.)

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```
Gen:    0 LD: 0.092 R2: 0.135 Fst: 0.523
Gen:  100 LD: 0.087 R2: 0.122 Fst: 0.187
Gen:  200 LD: 0.083 R2: 0.114 Fst: 0.151
Gen:  300 LD: 0.082 R2: 0.116 Fst: 0.152
Gen:  400 LD: 0.080 R2: 0.112 Fst: 0.124
Gen:  500 LD: 0.080 R2: 0.109 Fst: 0.256
Gen:  600 LD: 0.074 R2: 0.092 Fst: 0.281
Gen:  700 LD: 0.073 R2: 0.090 Fst: 0.258
Gen:  800 LD: 0.075 R2: 0.095 Fst: 0.245
Gen:  900 LD: 0.079 R2: 0.108 Fst: 0.119
Gen: 1000 LD: 0.070 R2: 0.088 Fst: 0.000
True
>>>
```

A penetrance model

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A penetrance model with two interating loci

	BB	Bb	bb
AA	0.1	0.1	0.5
Aa	0.1	0.1	0.5
aa	0.5	0.5	0.1

```
>>> def myPene(geno):
...     'geno is the genotype at the two given loci'
...     loc1 = geno[0] + geno[1]
...     loc2 = geno[2] + geno[3]
...     if (loc1 == 2 and loc2 < 2) or \
...         (loc1 < 2 and loc2 == 2):
...         return 0.1
...     else:
...         return 0.5
```

Apply this model

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```
>>> pop = population(subPop=[1000], loci=[6])
>>> # initialize the population
>>> InitByFreq(pop, [0.1, 0.9])
>>> # apply penetrance and obtain affection status
>>> PyPenetrance(pop, loci=[3, 5], func=myPene)
>>> # draw case control sample
>>> (sample,) = CaseControlSample(pop, cases=3, controls=3)
>>> # save sample in Merlin QTDT format
>>> from simuUtil import SaveQTDT
>>> SaveQTDT(sample, output='sample', affectionCode=['U', 'A'],
...     fields=['affection'])
>>> # have a look at the sample in Merlin-QTDT Format
>>> print open('sample.map').read()
CHROMOSOME MARKER POSITION
1       loc1-1  1.000000
1       loc1-2  2.000000
1       loc1-3  3.000000
1       loc1-4  4.000000
1       loc1-5  5.000000
1       loc1-6  6.000000
```

Generated sample

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```
>>> print open('sample.dat').read()
A       affection
M       loc1-1
M       loc1-2
M       loc1-3
M       loc1-4
M       loc1-5
M       loc1-6

>>> print open('sample.ped').read()
1 1 0 0 1 A 1 2 2 2 2 2 2 2 2 2 2 2
2 1 0 0 1 A 2 2 2 2 2 1 2 2 2 2 2 2
3 1 0 0 1 A 2 2 2 2 2 2 2 2 2 2 2 2
4 1 0 0 1 U 2 2 2 2 2 2 2 2 2 2 2 1
5 1 0 0 1 U 2 2 2 2 2 1 2 1 1 2 2 2
6 1 0 0 2 U 2 2 2 2 2 2 2 2 2 1 2 2

>>>
```

Calculate effective number of alleles

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The effective number of alleles can be estimated from a population by

$$\hat{n}_e = \left(\sum_{i>0} \left(\frac{f_i}{f_0} \right)^2 \right)^{-1} = \frac{f_0^2}{\sum_{i>0} f_i^2}$$

where f_i is the frequency of allele i, and $f_0 = \sum_{i>0} f_i$ is the total disease allele frequency (assuming 0 is the only wildtype allele).

```
>>> def Ne(pop, loci):
...     'Calculate effective number of alleles'
...     Stat(pop, alleleFreq=loci)
...     pop.dvars().Ne = {}
...     v = pop.dvars().alleleFreq
...     for locus in loci:
...         f0 = 1 - v[locus][0]
...         Ne = f0*f0/sum([x*x for x in v[locus][1:]])
...         pop.dvars().Ne[locus] = Ne
...     return True
```

Use a Python operator

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```
>>> simu = simulator(
...     population(1000, loci=[1], infoFields=['fitness']),
...     randomMating())
>>> simu.evolve(
...     preOps = [ initByFreq([0.1]*10) ],
...     ops = [
...         maSelector(locus=0, fitness=[1, 0.999, 0.998]),
...         pyOperator(func=Ne, param=[0], step=100),
...         pyEval(r'"Ne=%.3f\n" % Ne[0]', step=100),
...     ],
...     end=500
... )
Ne=8.936
Ne=5.156
Ne=4.824
Ne=2.830
Ne=4.179
Ne=3.897
True
>>>
>>>
```

scripts/loadHapMap.py

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Load genotypes from HapMap data file to an existing population

```
def load_population(pop, ch, type):
    '''Load population from file, with type (subpopulation type)
    subPop = {'CEU':0, 'YRI':1, 'JPT+CHB':2}[type]
    file = genotype_file % (ch, type, rev)
    print 'from %s...' % file
    for line_no,line in enumerate(open(file).readlines()):
        genotype = [int(x) for x in line.split()]
        ind = line_no / 2
        ploidy = line_no % 2
        ind = pop.individual(ind, subPop)
        for i,g in enumerate(genotype):
            # always chromosome 0, because each population has o
            ind.setAllele(g, i, ploidy)
```

Pick markers from HapMap data

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```
>>> genes = [
...     "rs1042522",
...     "rs1625895",
...     "rs1799793",
... ]
>>> pops = []
>>> for i in range(1, 23):
...     print "Loading hapmap chromosome %d..." % i
...     pop = LoadPopulation('hapmap_%d.bin' % i)
...     markers = []
...     for name in genes:
...         try:
...             idx = pop.locusByName(name)
...             markers.append(idx)
...         except:
...             pass
...     if len(markers) > 0:
...         markers.sort()
...         pop.removeLoci(keep=markers)
...         pops.append(pop)
>>> all = MergePopulationsByLoci(pops)
```

Use of simuOpt.py

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```
options = [
    {'arg':'h',
     'longarg':'help',
     'default':False,
     'description':'Print this usage message.',
     'jump':-1
    },
    {'arg':'s:',
     'longarg':'size=',
     'default':1000,
     'label':'Population Size',
     'allowedTypes':[types.IntType, types.LongType],
     'validate':simuOpt.valueGT(0),
     'description':'Population size'
    },
    {'arg':'r:',
     'longarg':'recRate=',
     'default':0.01,
     'label':'Recombination Rate',
     'allowedTypes':[types.FloatType],
     'description':'Recombination rate',
     'validate':simuOpt.valueBetween(0.,1.),
    },
]
```

Process parameters

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```
# get all parameters
allParam = simuOpt.getParam(options, __doc__)

if len(allParam) > 0:    # successfully get the params
    (help, popSize, endGen, recRate, numRep, saveFigure,
    saveConfig, method, verbose) = allParam
else:
    sys.exit(0)

if saveConfig != '':
    simuOpt.saveConfig(options, saveConfig, allParam)

if help:
    print simuOpt.usage(options, __doc__)
    sys.exit(1)
```

Parameter dialog

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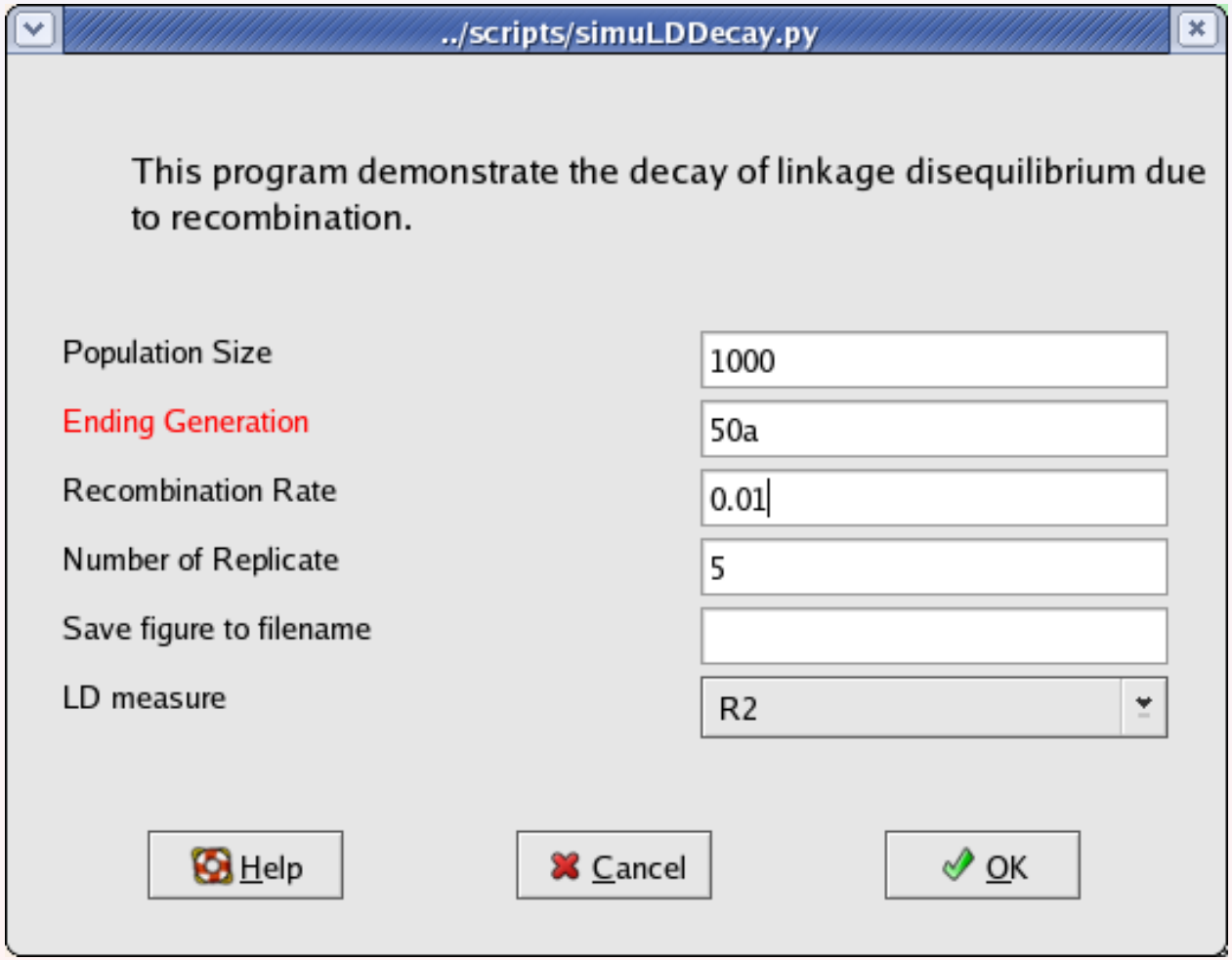

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simuNeutralSNPs.py

simuForward.py

simuComplexDisease.py

simuCluster.py

4 Bundled Scripts

- simuLDDecay.py
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simuLDDecay.py

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simuComplexDisease.py

simuCluster.py

- simulate the decay of linkage disequilibrium with recombination
- can control population size, recombination rate, number of replicates and generations
- use `simuRPy.py` to visualize the decay of LD

simuNeutralSNPs.py

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simuCluster.py

- simulate the evolution of unlinked SNP markers
- observe the distribution of minor allele frequencies
- no selection

simuForward.py

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- Traditional forward-time simulation
- Use a dynamic-selector to control disease allele frequencies in a disease introduction stage
- Restart simulation when a disease allele get lost

simuComplexDisease.py

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- New forward-time simulation method (Peng, 2007)
- Simulate the trajectory of disease allele frequencies backward in time
- Controlled forward-time simulation method that follows simulated disease allele frequency

simuCluster.py

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simuCluster.py

- A utility script to help run simuPOP scripts on a cluster system
- User provides a template script and a list of paramters
- This script generates scripts and submit the jobs

Acknowledgments

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- M.D. Anderson Cancer Center High Performance Cluster
- BP was supported in part by a grant CA75432 from NCI
- Yaji Xu helped with all the figures in this talk

For further reading

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Bo Peng and Marek Kimmel (2005). simuPOP: a forward-time population genetics simulation environment. *Bioinformatics,* 21:3686–3687

Bo Peng and Marek Kimmel (2007) Simulations provide support for the common disease common variant hypothesis. *Genetics.* 175:763-776.

Bo Peng, Christopher I. Amos and Marek Kimmel (2007) Forward-time simulations of complex human diseases. *PLoS Genetics,* 3(3):e47.

That is all

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For more details, please check out

- simuPOP user's guide
- simuPOP reference manual
- Another presentation about the details of each simuPOP components

Under the doc directory of your simuPOP distribution.