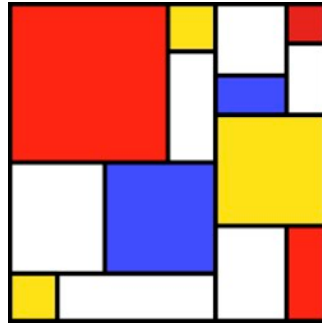


Modeling Population and Quantitative Genetics in SLiM

forward genetic simulation software

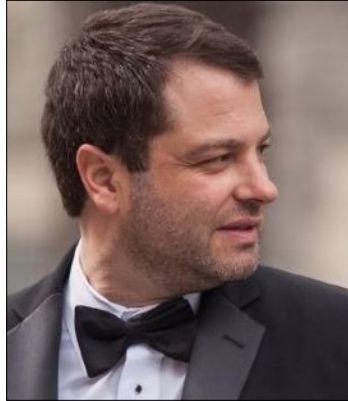


KITP, 2022

SLiM Contributors



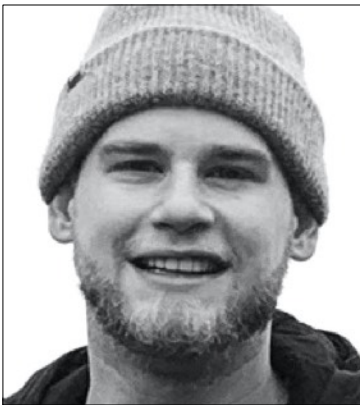
Ben Haller



Philipp Messer



Peter Ralph



Jared Galloway



Jerome Kelleher



Ben Jeffery

... and many more!

Talk outline

- What is SLiM? Why use SLiM?
- An introduction to Eidos and SLiM
- A survey of example models
- Population-genetic models in SLiM
- Quantitative-genetic models in SLiM
- Closing remarks

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Forward genetic simulation

- **“Forward”**:
 - runs forward from an initial state
(vs. coalescent methods)
- **“Genetic”**:
 - explicit loci on a chromosome
(vs. phenotypic simulations)
- **“Simulation”**:
 - individual-based modeling
(vs. analytical modeling)

Why do simulations?

- Fitting **empirical** population genomic data
 - analyzing past evolutionary forces
 - predicting future evolution
- Analyzing **theoretical** evolutionary models
 - predicting the consequences of a new theory
 - comparing multiple theories
- Developing **statistical** methods
 - testing a method's accuracy, bias, or power
 - generating datasets for machine learning

Why do *forward* simulations?

- **Evolution is complex:**
 - complex demography and population structure
 - non-random mating and complex mating systems
 - spatial structure and non-random dispersal
 - spatial and temporal variation in selection
 - frequency-dependent selection, kin selection, etc.
 - realistic genetic/chromosomal structure
 - epistasis, polygenic traits, pleiotropy
 - multiple loci under selection
 - variable recombination / mutation rate

Why use SLiM?

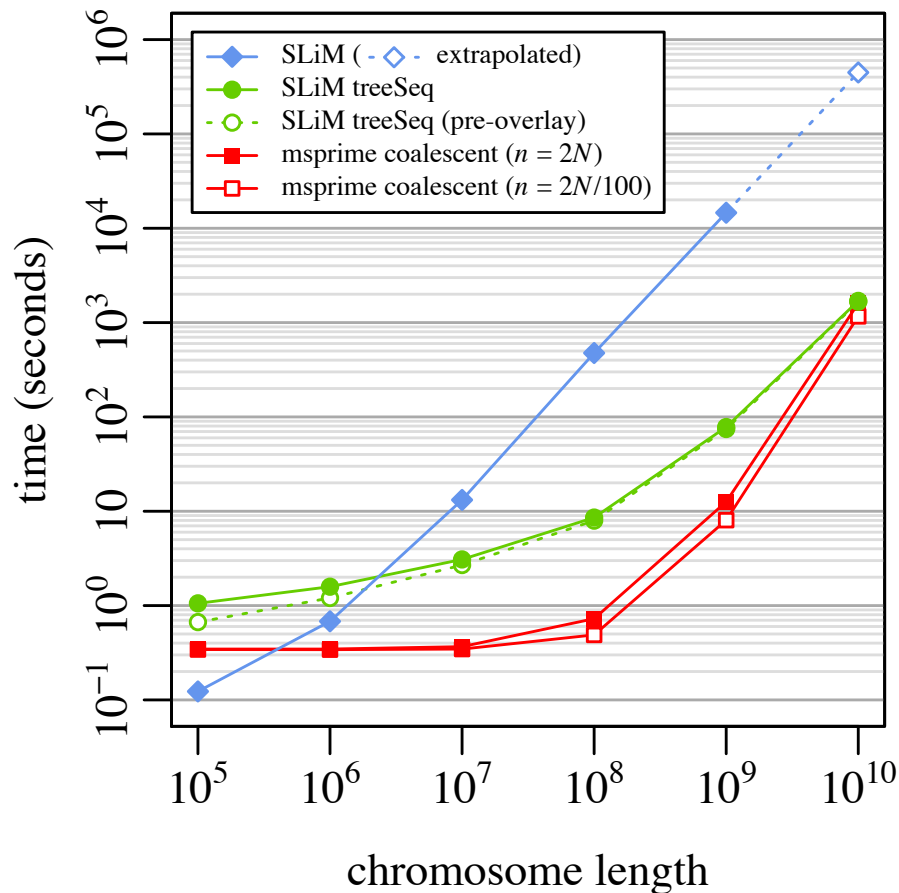
Why use SLiM?

- Flexible and customizable with Eidos
 - scriptability means there are (almost) no limits
 - similar to R in its syntax and function names
 - ends statements with semicolons; zero-based!

```
x = 0;  
for (i in 1:10)  
    x = x + i;  
print(x);
```

Why use SLiM?

- Very fast: SLiM is highly optimized



neutral simulation
mean over 10 replicates
 $N = 500$ diploids
 $r = 10^{-8}$
 $\mu = 10^{-7}$

run to the expected time for
coalescence ($\sim 3N$ to $\sim 15N$)

Why use SLiM?

- Interactive and graphical
 - easy to visualize / debug / explore

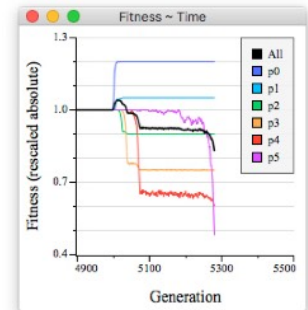
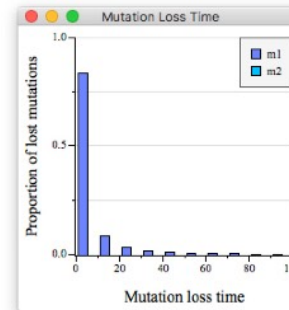
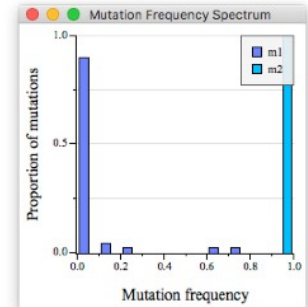
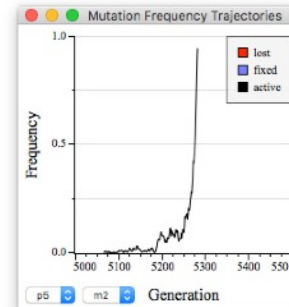
The screenshot shows the SLiM GUI with the following components:

- Simulation Window:** Displays a chromosome with a yellow grid representing mutations. The x-axis is labeled "Generation" and ranges from 0 to 99999. A progress bar at the bottom indicates the current generation is 2001.
- Input Commands:** A text area containing SLiM code for setting up a neutral simulation with 500 individuals and 10 genomes.
- Run Output:** A window showing the simulation's progress, including the number of mutations, the state of the population, and the results of the simulation.

```
// set up a simple neutral simulation
initialize() {
  initializeMutationRate(1e-7);
  // m1 mutation type: neutral
  initializeMutationType("m1", 0.5, "f", 0.0);
  // g1 genomic element type: uses m1 for all mutations
  initializeGenomicElement("g1", m1, 1.0);
  // uniform chromosome of length 100 kb with uniform recombination
  initializeGenomicElement(g1, 0, 99999);
  initializeRecombinationRate(1e-8);
}
// create a population of 500 individuals
1 {
  sim.addSubpop("p1", 500);
}
// output samples of 10 genomes periodically, all fixed mutations at end
22 1000 late() { p1.outputSample(10); }
23 2000 late() { p1.outputSample(10); }
24 2000 late() { sim.outputFixedMutations(); }
25
```

Run Output:

```
24 19778 m1 38974 0 0.5 p1 1992 1
Genomes:
p1:0 A 0 1 2 3 4 5
p1:1 A 6 2 4 7
p1:2 A 8 9 10 11 12 13 14 15 4 16 17
p1:3 A 0 1 2 3 4 5
p1:4 A 8 9 10 18 19 11 12 13 20 15 4 21 16 17
p1:5 A 8 9 10 19 11 12 13 15 4 16 17
p1:6 A 0 22 1 2 3 23 4
p1:7 A 0 9 10 19 11 12 13 15 4 16 17
p1:8 A 0 10 24 19 11 12 25 13 15 4 16 26 17
p1:9 A 8 0 10 27 11 12 13 14 15 4 16 17
#OUT: 2000 F
Mutations:
0 658 m1 11823 0 0.5 p1 69 1378
1 10702 m1 38821 0 0.5 p1 1092 1923
2 9748 m1 41089 0 0.5 p1 993 1923
3 6859 m1 45670 0 0.5 p1 701 1923
4 3786 m1 68033 0 0.5 p1 391 1923
5 2671 m1 78431 0 0.5 p1 276 1923
6 8168 m1 74927 0 0.5 p1 834 1923
7 3378 m1 78651 0 0.5 p1 350 1923
8 12523 m1 96887 0 0.5 p1 1275 1923
9 12511 m1 97265 0 0.5 p1 1273 1923
```



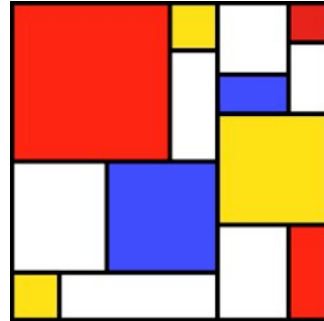
Why use SLiM?

- Open source on GitHub, GPL license
 - free, reusable, shareable, debugged, easy!

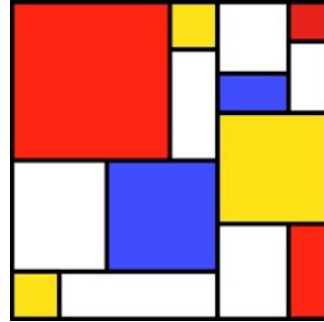


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live demo



An introduction to Eidos

Data types

- `NULL`: no explicit value
- `logical`: a Boolean true/false value (`T/F`)
- `integer`: a 64-bit signed integer (`10, -27`)
- `float`: a floating-point number (`10.0, -2.7`)
- `string`: a sequence of characters (`"foo"`)
- `object`: an instance of a class (`Individual`)

Operators

- Arithmetic: +, -, *, /, %, ^, : $6 + 2*7$
- Logical: &, |, ! $T \& !F$
- Comparison: <, >, <=, >=, ==, != $2+2 == 4$
- Assignment: = $x = 8$
- Precedence and function call: () $(6+2) * 7$
- Subset: [] $x[5]$
- Property access and method call: . $foo.bar$

Control flow

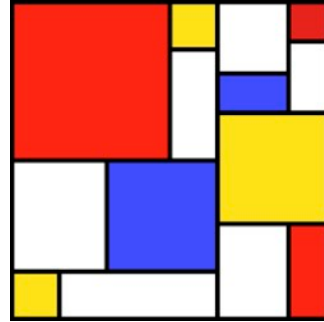
- **if-else:** conditional execution
 - `if (condition) statement; else statement;`
- **while:** loop on a condition, 0+ times
 - `while (condition) statement;`
- **do-while:** loop on a condition, 1+ times
 - `do statement; while (condition);`
- **for:** loop over the values in a vector
 - `for (i in vector) statement;`

Built-in functions

- **Math:** `abs()`, `ceil()`, `log()`, `setUnion()`, ...
- **Statistics:** `max()`, `mean()`, `sd()`, `cov()`, ...
- **Distributions:** `rnorm()`, `rpois()`, `runif()`, ...
- **Vectors:** `c()`, `rep()`, `seq()`, `sample()`, ...
- **Values:** `all()`, `any()`, `identical()`, `sort()`, ...
- **Output:** `cat()`, `print()`, `paste()`, `str()`, ...
- **Types:** `isFloat()`, `asFloat()`, ...
- **Filesystem:** `readFile()`, `writeFile()`, ...

Objects, properties, methods

- Objects represent **entities**:
 - e.g., individuals, mutations, subpopulations
- Objects have **properties**:
 - attributes like age, sex, spatialPosition
 - `individual.age` returns the age of individual
 - `individual.age = 10`; changes its age
- Objects have **methods**:
 - methods perform complex operations
 - `individual.containsMutations(muts)`



An introduction to SLiM

SLiM Eidos classes

- Chromosome hierarchy:
 - Chromosome
 - MutationType
 - GenomicElementType
 - GenomicElement
- Other classes:
 - InteractionType
 - LogFile
 - SLiMEidosBlock
 - SLiMgui
- Community hierarchy:
 - Community
 - Species
 - Subpopulation
 - Individual
 - Genome
 - Mutation
 - Substitution
- Popgen utilities, nucleotide utilities, etc.

The chromosome hierarchy

Genomic elements, genomic element types, and mutation types

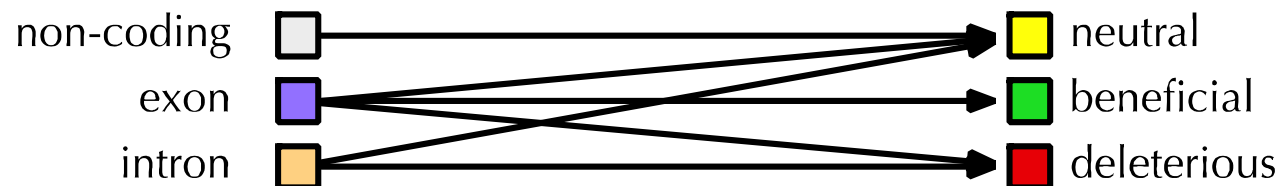
- The chromosome defines the genetic structure
- It is a sequence of elements (`GenomicElement`)
- Each element has a type (`GenomicElementType`)
- Each type draws from a DFE (`MutationType`)

Chromosome: a mosaic of genomic elements



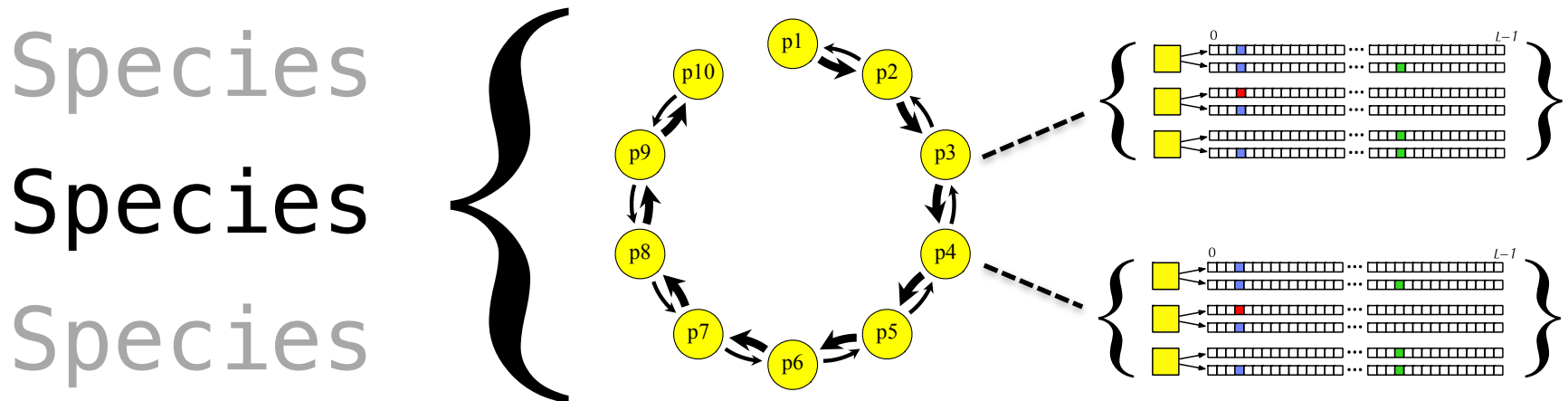
Genomic element types

Mutation types



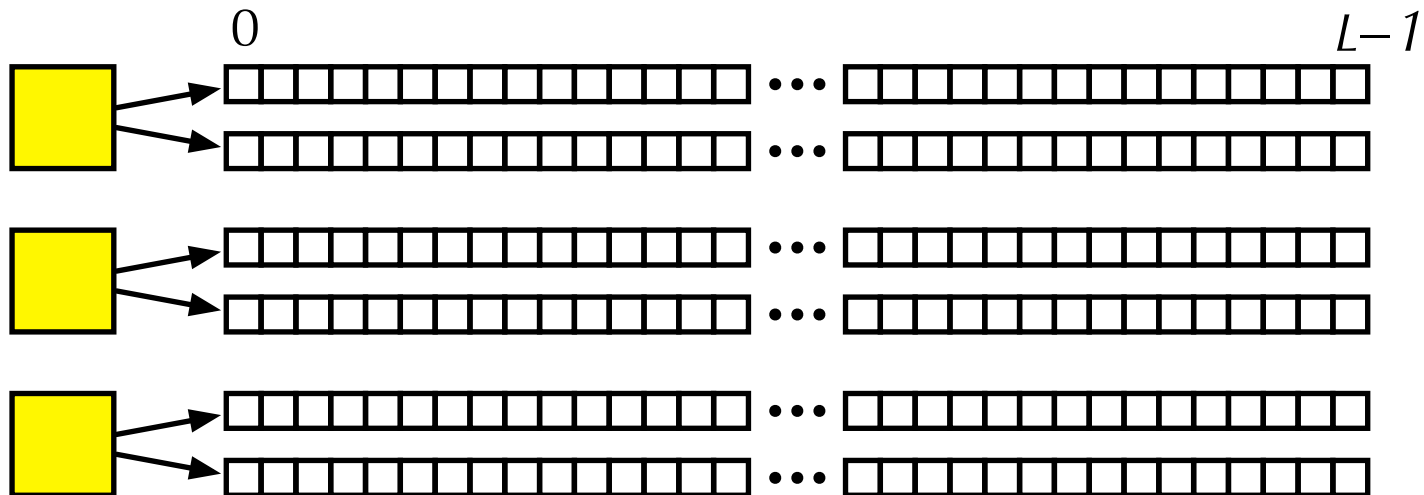
The community hierarchy

- The *community* contains one or more *species*
- Each species contains *subpopulations*
- Each subpopulation contains *individuals*
- Each individual contains *genomes*
- Each genome contains *mutations*



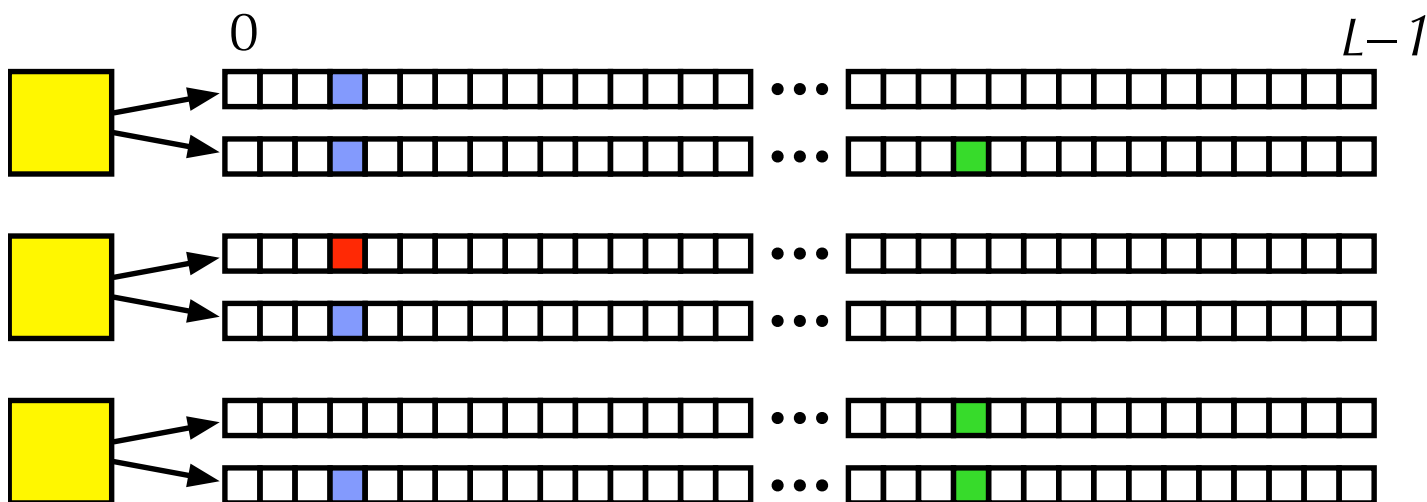
Individuals and genomes

- Individuals (class `Individual`) are organisms
- Individuals are born, mate, die, ...
- Each individual has two genomes (class `Genome`)
- Each genome has L discrete base positions



Mutations

- Mutations (class `Mutation`) live in genomes
- Genomes begin empty (the *ancestral* state)
- Mutations represent a *non-ancestral* allele (SNP)
- Mutations have properties: selection coefficient



The “SLiM core”

- SLiM is divided into the “core”...
 - Optimized C++ to run the tick cycle
 - Default behaviors for simple models:
 - Fitness, mate choice, gamete generation, mutation, recombination, mortality, ...
- ... and everything else, in Eidos script:
 - Events (`first()`/`early()`/`late()`)
 - Callbacks

SLiM callbacks

- `fitness()`: individual-based fitness effects
- `mateChoice()`: non-random mating effects in WF models
- `reproduction()`: scripted reproduction in nonWF models
- `modifyChild()`: individual customization of offspring
- `mutation()`: customization of the mutational process
- `recombination()`: customization of recombination
- `survival()`: influencing mortality in nonWF models
- `interaction()`: spatial interactions (competition, mating)

WF versus nonWF

- SLiM supports two different model types:
 - **WF**: Wright–Fisher
 - **nonWF**: non-Wright–Fisher
- Differences:
 - tick cycles
 - offspring generation
 - population regulation
 - age structure
 - fitness models
 - demography
 - mate choice
 - migration

WF Models

- Population size is a parameter
- Population regulation is automatic
- Fitness affects mating probability
- Selection is soft (relative fitness)
- Non-overlapping generations
- No age structure
- Migration is due to parameters

nonWF Models

- Population size is emergent
- Population regulation is scripted
- Fitness affects viability/survival
- Selection is hard (absolute fitness)
- Generations can overlap
- Age structure is emergent
- Migration is scripted

Fitness

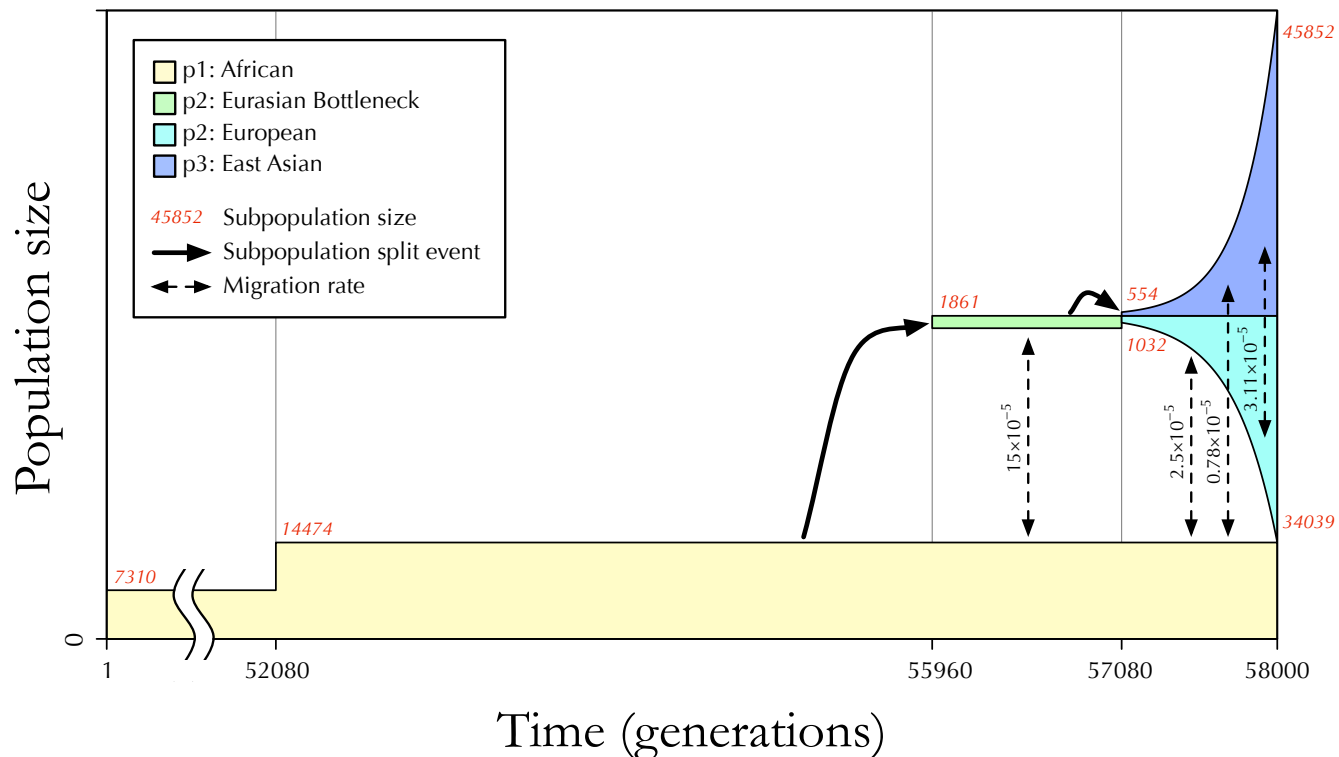
- Fitness is a multiplicative combination of *effects*
- Fitness effects come from:
 - mutations ($1 / 1+bs / 1+s$)
 - `fitness()` callbacks – *per mutation*
 - individual `fitnessScaling` values
 - subpopulation `fitnessScaling` values
- This allows:
 - QTLs, behavior, spatiotemporal variation...

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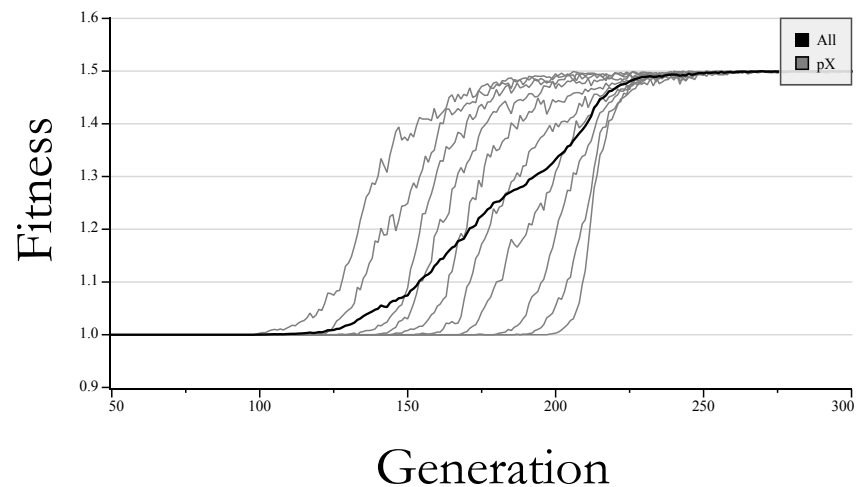
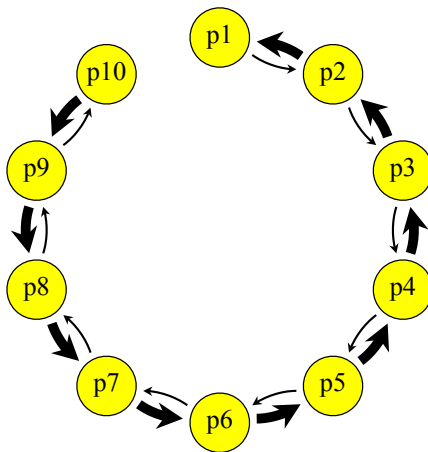
The Gravel model (5.4)

- Simulating human evolutionary history
- Demographic events, exponential growth



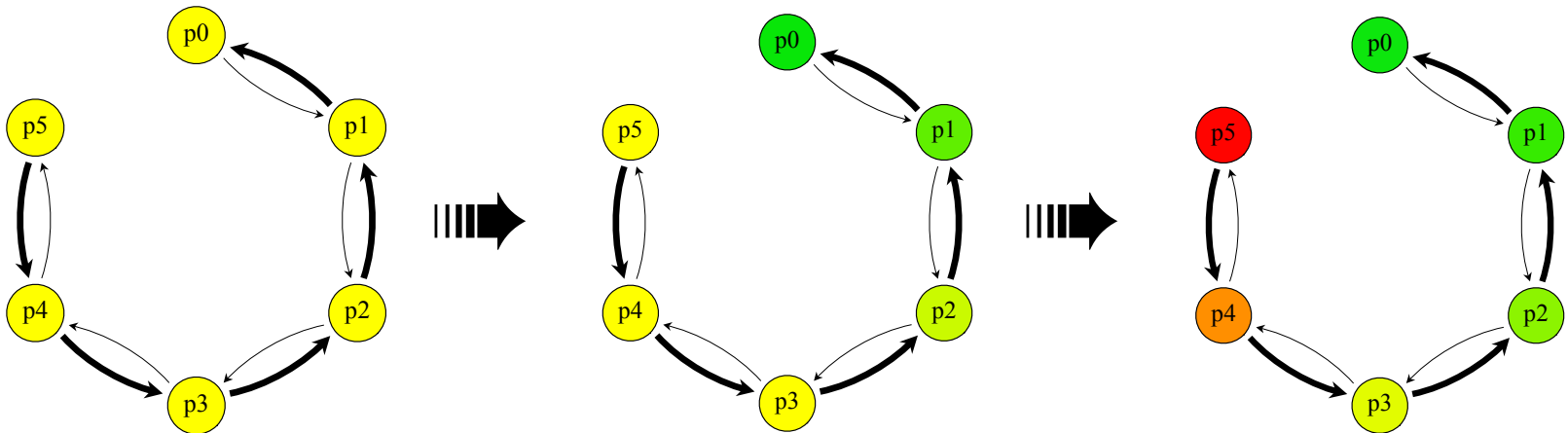
Introgression & sweeps (9.7)

- Introgression of a single introduced mutation
- Ten subpopulations connected by migration



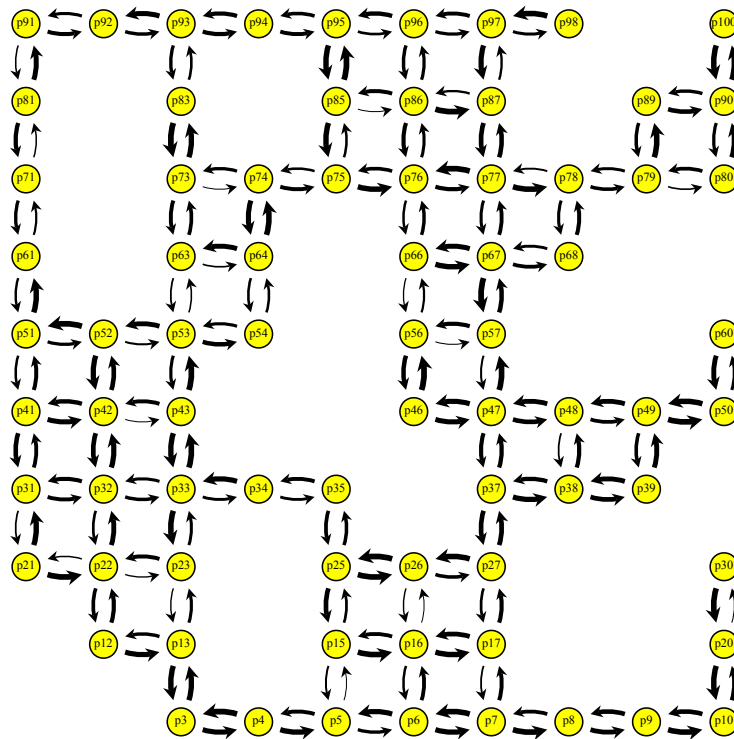
Gene drives (12.3)

- Simulating CRISPR gene drive
- Fixes despite negative fitness effects
- Fixes despite going against migration



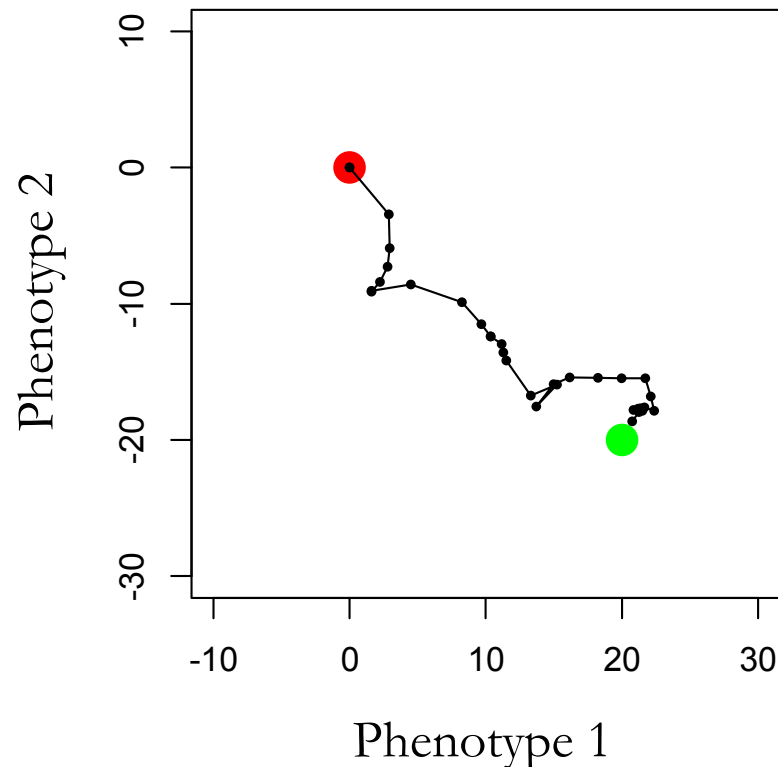
Metapopulations (5.3.4)

- Many subpopulations connected by migration
- The connection pattern can be spatial, or not



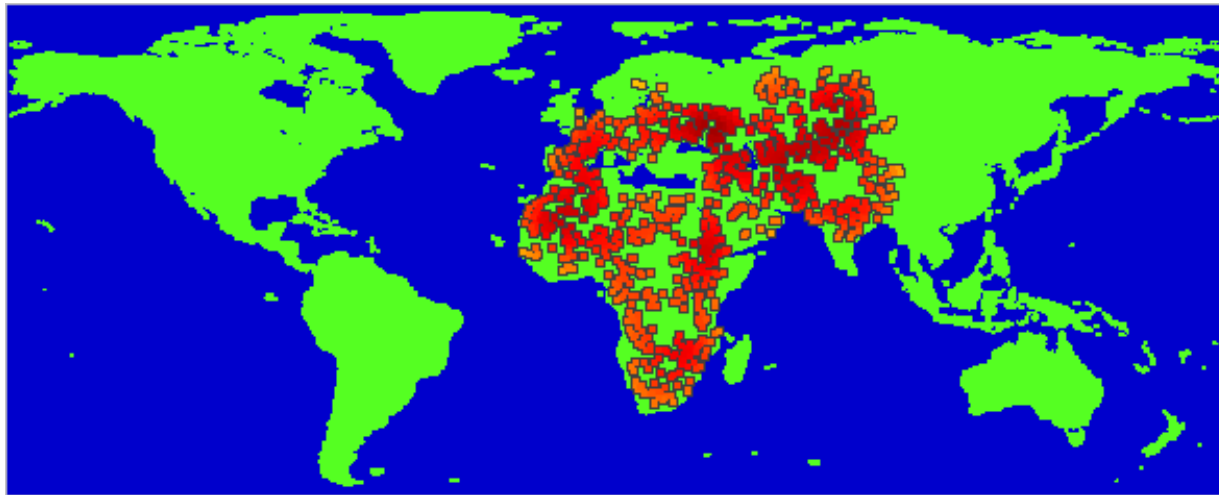
Adaptive walks (14.8)

- A QTL-based model with pleiotropy (M-matrix)
- Two phenotypic traits defined by additive QTLs



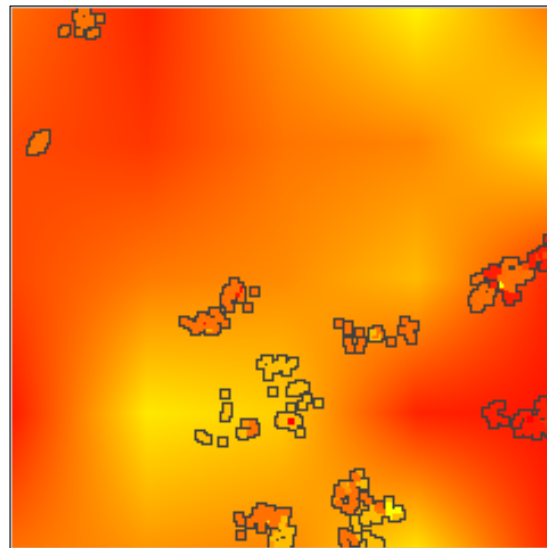
Continuous space (15.10)

- Individuals live in a continuous 2-D space
- A landscape map of the world is used
- Population expansion out of Africa



Local adaptation (15.11)

- Individuals live in a continuous 2-D space
- A map defines a heterogeneous environment
- Adaptation to the local environment results



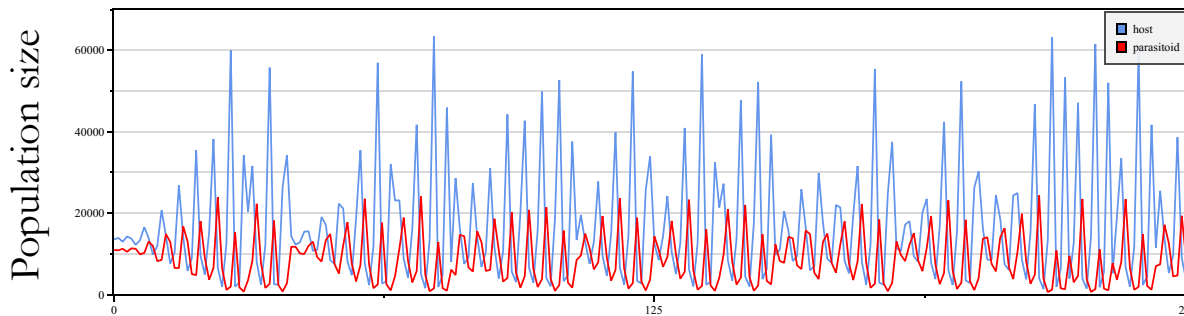
Nucleotide-based models (18.1)

- Track the nucleotide sequence of every genome
- Mutations have an associated nucleotide
- Mutation rates are sequence-dependent
- Realistic gene conversion, including gBGC

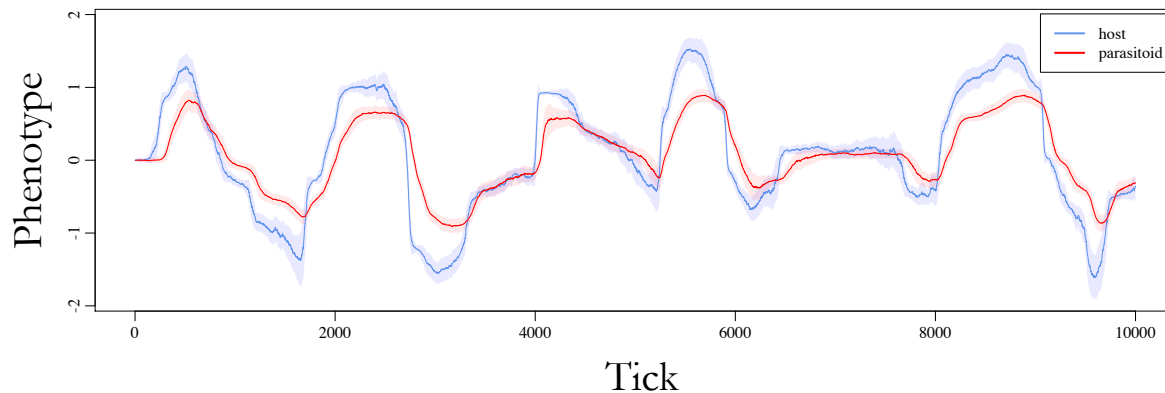
```
GAATGTCGGTTAGAGCAACCTAGCTTCTCAGATCGCAATA
GAATGTCCGTTAGAGCAACCTAGCTTCTCAGATGGCTATA
GAATGTCCGTTAGAGCAACCTAGCTTCTCAGATGGCCATA
GAATGTCGGTTAGAGCATCCTAGCTTCTCAGATCGCAATA
GAATGTCGGTTAGAGCAACCTAGCTTCTCAGATCGCAATA
GAATGTCCGTTAGAGCAACCTAGCTTCTCAGATGGCAATA
GAATGTCGGTTAGAGCATCCTAGCCTCTCAGATGGCAATA
GAATGTCGGTTAGAGCATTCCTAGCTTCTCAGATCGCAATA
```

Multispecies models (19.4 & 19.6)

- Simulate more than one species in a model
- Ecology: competition, predation, parasitism, ...
- Coevolutionary and eco-evolutionary dynamics



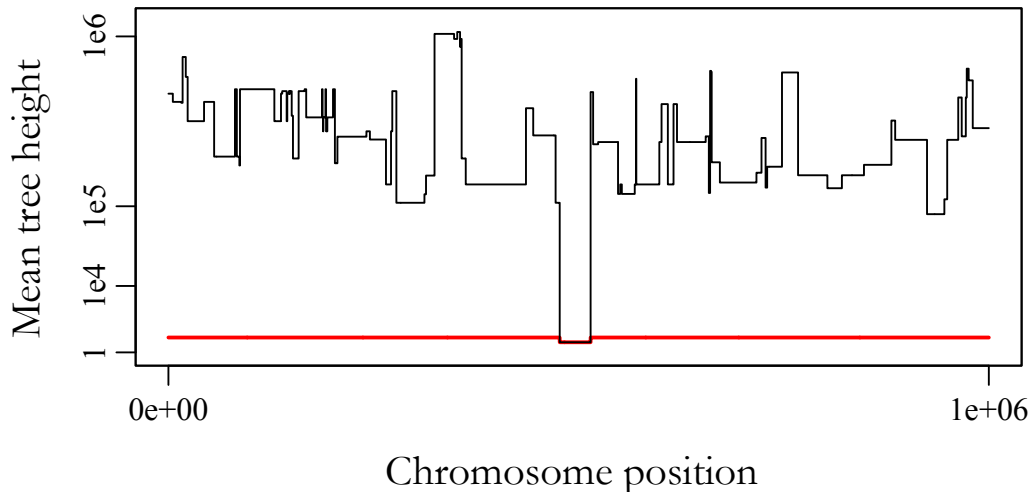
19.4: Host-parasitoid population size cycling



19.6: Red Queen coevolutionary dynamics

Tree sequences & ancestry (17.10)

- Tracking the ancestry tree at every position
- Mean tree height is a proxy for diversity at a site
- After a sweep, diversity is lowest near the sweep
- Recapitation constructs neutral burn-in history



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Population-genetic models

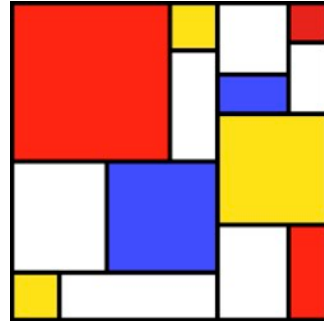
- Demography:
 - Discrete subpopulations with migration
 - Continuous space with dispersal
- Ploidy:
 - Diploid, haploid, haplodiploid*, ...*
- Sex and mating:
 - Hermaphrodites, separate sexes, X/Y, ...*
 - Biparental sexual mating
 - Cloning, selfing, horizontal gene transfer*, ...*

Population-genetic models

- Any chromosome length
- Any number of chromosomes*
- Any number of loci and alleles
- Any recombination-rate map
- Any mutation-rate map
- Any distributions of fitness effects
- Any individual effects* on fitness, mortality, mate choice, recombination, migration, dispersal, mutation, ...

Population-genetic models

- Selective sweeps
 - partial or full
 - conditional on fixation or establishment
 - soft and hard sweeps of various kinds
- Background selection
- Local adaptation
- Introgression
- Reproductive isolation (partial or full)
- Speciation



live demo

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Quantitative Traits

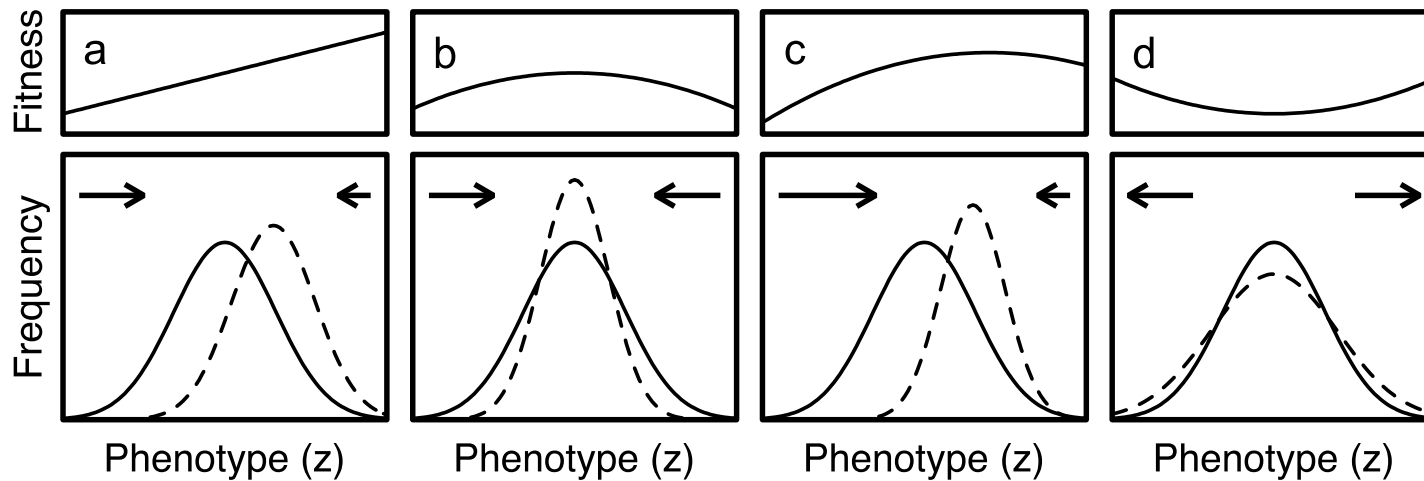
- Mendelian traits:
 - governed by a single locus
 - produce discrete outcomes
 - can be modeled with selection coefficients
- Quantitative traits:
 - governed by multiple loci: QTLs
 - produce continuous variation (e.g., height)
 - need to be modeled via **phenotype**

Quantitative Traits

- Phenotype
 - calculated from QTL effects
 - **additive effects** are central (breeding value)
 - non-additive effects can also be modeled
 - dominance, epistasis
 - environmental noise can be added
 - phenotypic plasticity can be included
 - the final result: a **phenotypic trait value**

Quantitative Traits

- Fitness
 - a function of phenotypic trait value
 - often modeled as a **fitness function**



directional

stabilizing

both

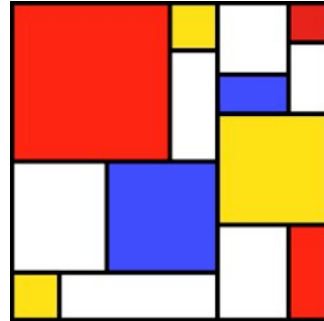
disruptive

others:
balancing
truncating
“squashed
stabilizing”

etc.

The Big Picture

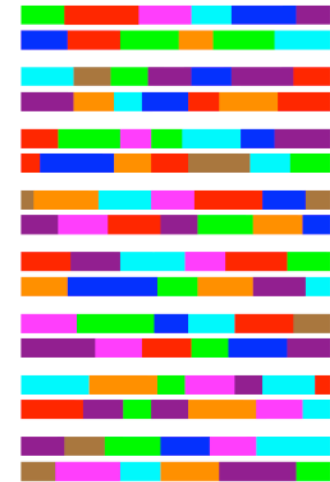
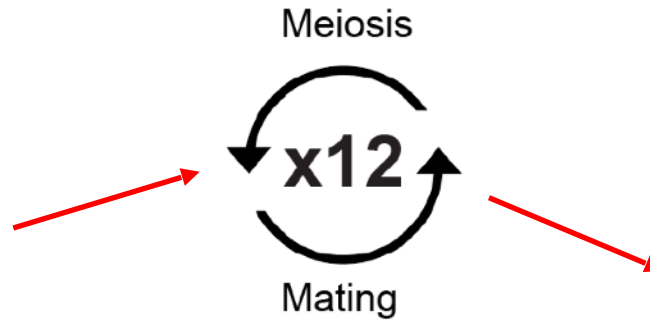
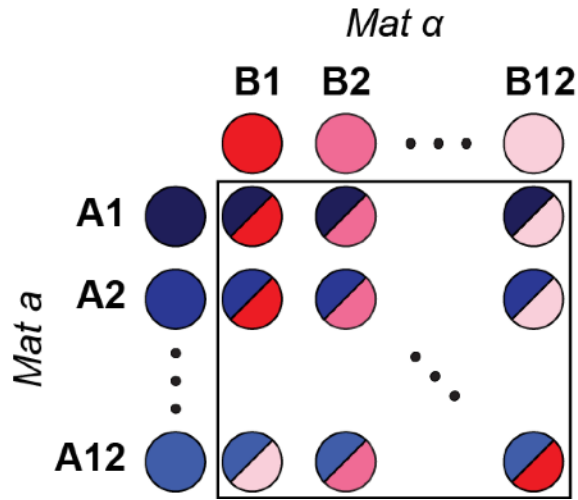
- QTL mutations have an effect size
- Phenotype is the sum of all effects
- Fitness is some function of phenotype
- Fitness effects are assigned to individuals



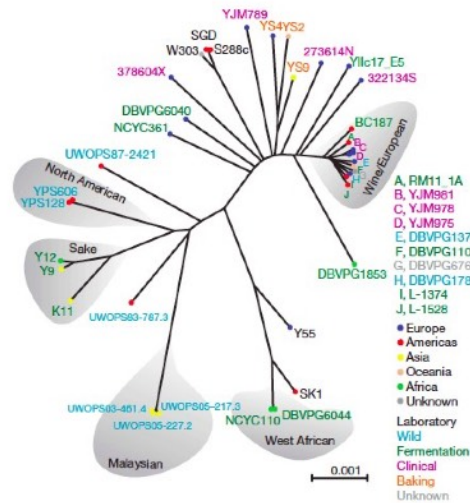
live demo

Surprise Guest Star
Tony Long!

Yeast E&R from a synthetic base population

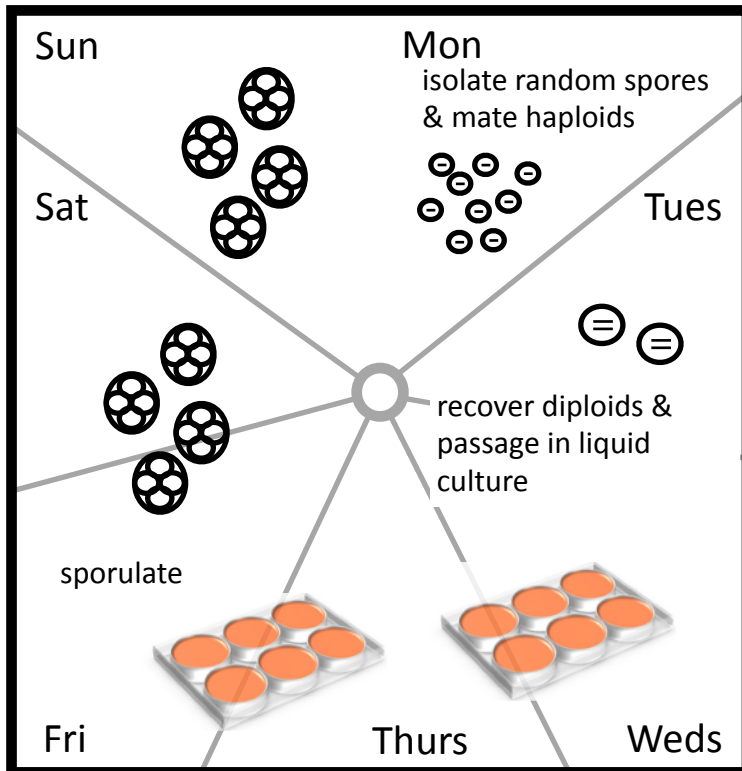


18-way synthetic recombinant population



Experimental Evolution Strategy

Complex E&R experiment

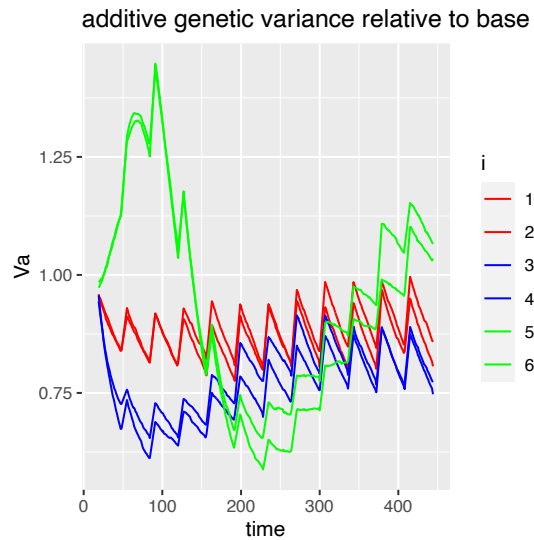
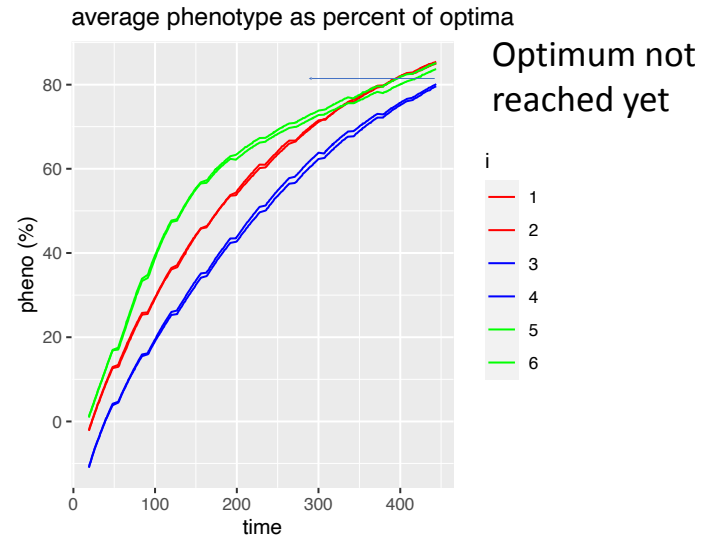
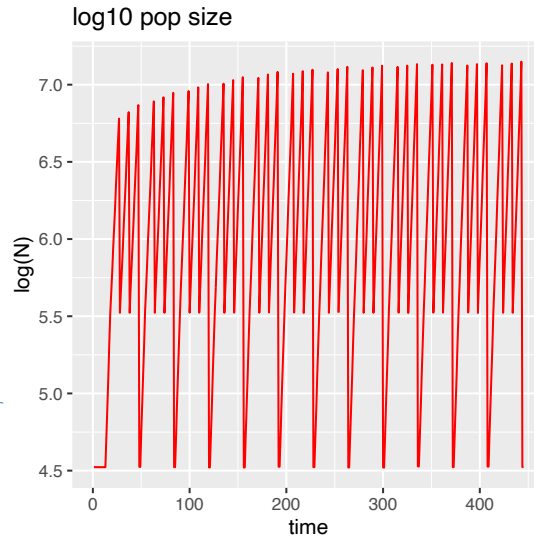


- Sex on Friday
- Recover spores and mate on Tuesday (bottleneck to $10^5 - 10^6$ cells)
- Asexual growth in media with chemical challenge
- 3 transfers per week (100-fold dilution)
- $10^7 - 10^9$ cells during selection/asexual growth

Would like quantitative predictions ... but this experiment seemed painful to model

SLIM!

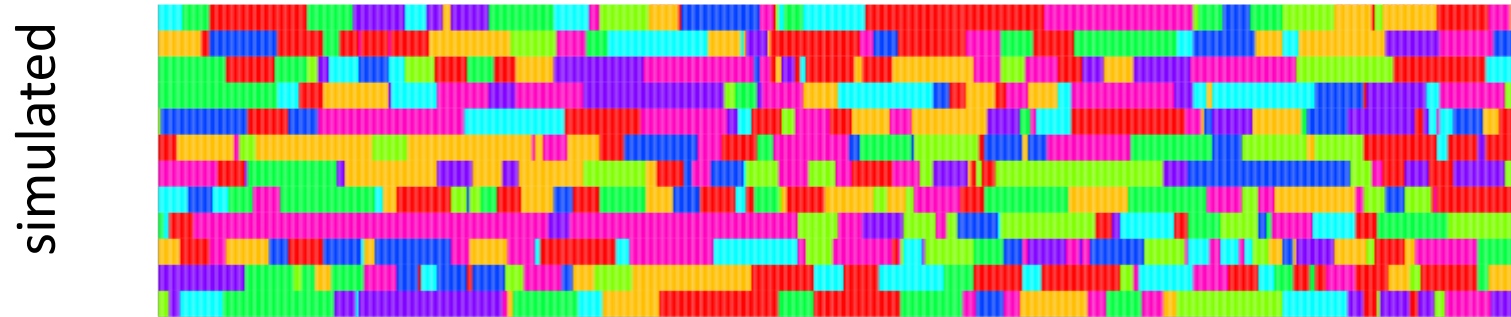
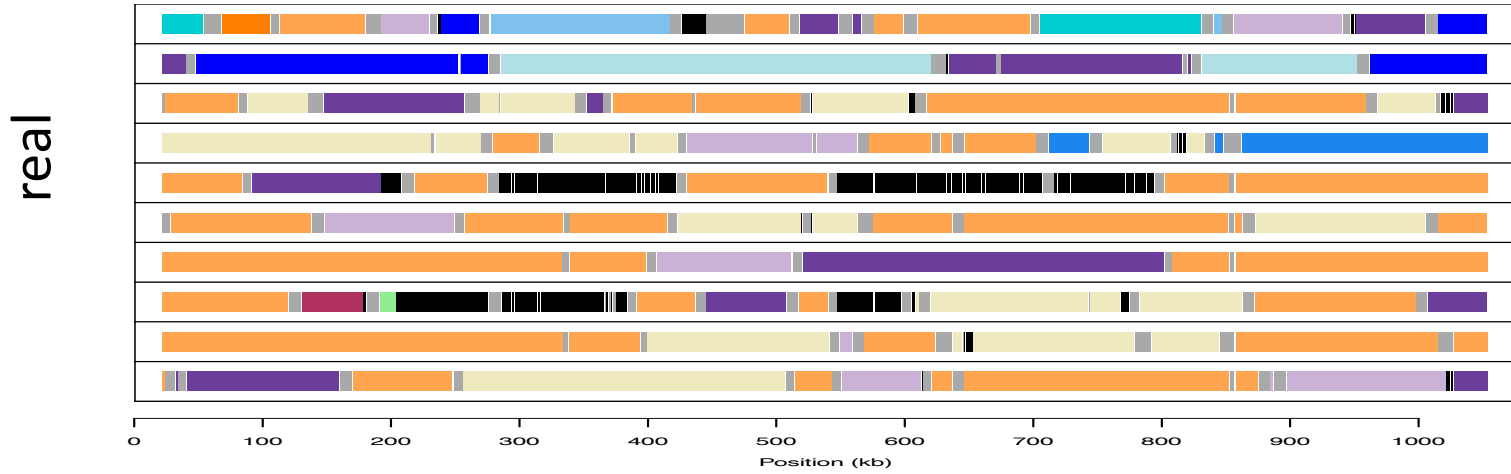
~30K, less than real



- 1800 SNPs
- 180 SNPs
- 18 SNPs

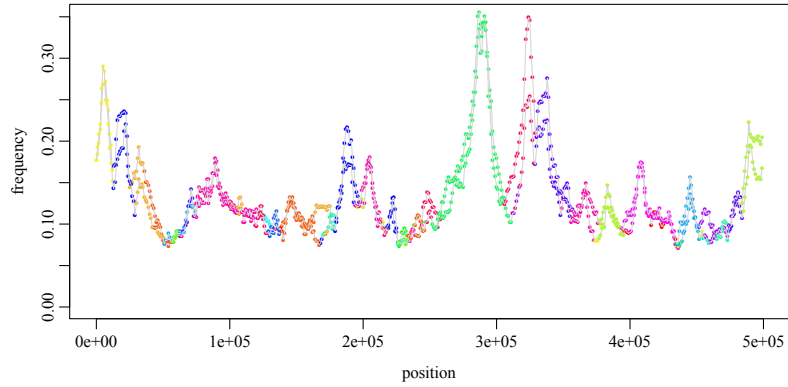
- 9 hours
- 25 Gb memory

haploid alleles for a single chromosome

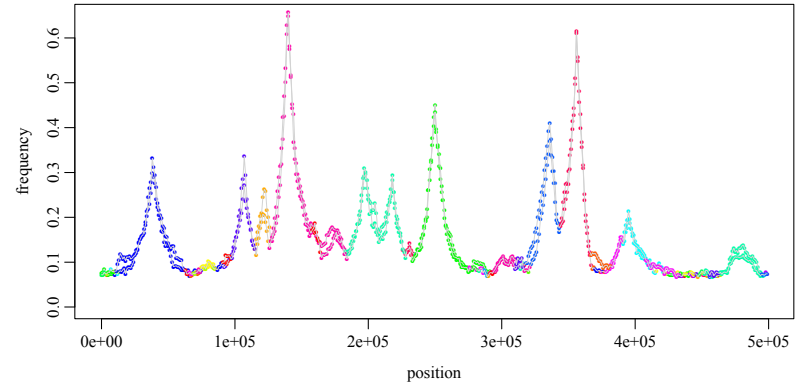


Pollock Plots

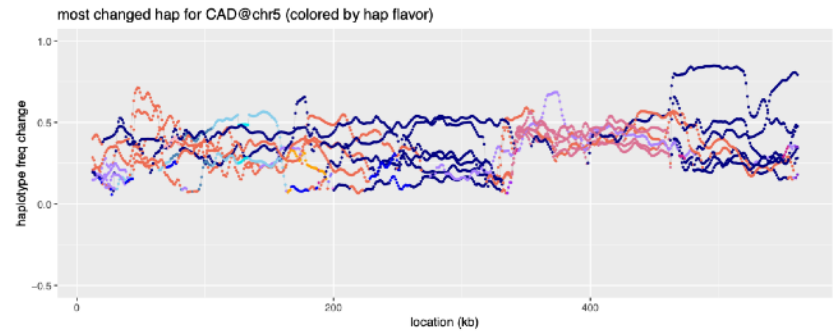
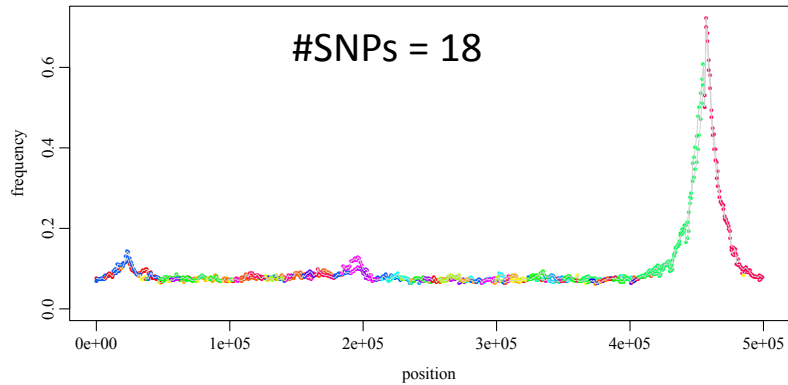
#SNPs = 1800



#SNPs = 180



#SNPs = 18



Talk outline

- What is SLiM? Why use SLiM?
- An introduction to Eidos and SLiM
- A survey of example models
- Population-genetic models in SLiM
- Quantitative-genetic models in SLiM
- Closing remarks

Resources



messerlab.org/slim/

bit.ly/slim-discuss

bhaller@mac.com

SLiM 3: Forward Genetic Simulations Beyond the Wright–Fisher Model

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Associate editor: Ryan Hernandez

Abstract

With the desire to model population genetic processes under increasingly realistic scenarios, forward genetic simulations have become a critical part of the toolbox of modern evolutionary biology. The SLiM forward genetic simulation framework is one of the most powerful and widely used tools in this area. However, its foundation in the Wright–Fisher model has

Wright–Fisher model overlapping generations in dispersal fitness-based survival SLiM 3, which contains “nonWF” model types scenarios and maps of environmental models to illustrate

Key words: eco-evolutionary dynamics, landscape

Introduction

Forward genetic simulation has played an important role in evolutionary biology. This model a wide range of scenarios include a high level of realism (Carvajal-Rodriguez 2014; Hoban 2014; Haller et al. 2018). The SLiM framework (Messer et al. 2014) has become a powerful tool for modeling the most widely used simulation

The National Science Foundation (NSF) Grant (DEB-1555504) supported this work. The National Science Foundation (NSF) Grant (DEB-1555504) supported this work. The National Science Foundation (NSF) Grant (DEB-1555504) supported this work.

Received: 10 September 2018 | Revised: 6 November 2018 | Accepted: 9 November 2018
DOI: 10.1111/1755-0998.12968

RESOURCE ARTICLE

WILEY **MOLECULAR ECOLOGY RESOURCES**

Tree-sequence recording in SLiM opens new horizons for forward-time simulation of whole genomes

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Funding information
National Science Foundation, Grant/Award Number: DEB-1262645; Grant/Award Number: DEB-1555504

Abstract

Evolutionary Modeling in SLiM 3 for Beginners

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Associate editor: Ryan Hernandez

Abstract

The SLiM forward genetic simulation framework has proved to be a powerful and flexible tool for population genetic modeling. However, as a complex piece of software with many features that allow simulating a diverse assortment of evolutionary models, its initial learning curve can be difficult. Here we provide a step-by-step demonstration of how to build a simple evolutionary model in SLiM 3, to help new users get started. We will begin with a panmictic neutral model, and build up to a model of the evolution of a polygenic quantitative trait under selection for an environmental phenotypic optimum.

SLiM Workshops



Sweden, 2019



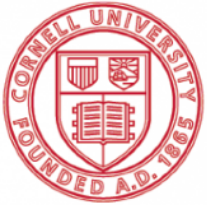
Iceland, 2020



UK, 2019

Now available online, free, at messengerlab.org/slim/

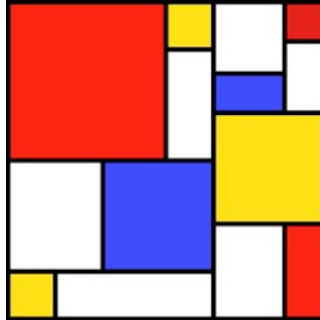
Acknowledgements



Cornell University



Thanks to Simon Aeschbacher, Pamela Alamilla, Rodrigo Pracana Fragoso De Almeida, Jorge Amaya, Bill Amos, Chenling Antelope, Jaime Ashander, Hannes Becher, Emma Berdan, Jeremy Berg, Gertjan Bisschop, Tom Booker, Gideon Bradburd, Jason Bragg, Vince Buffalo, Yoann Buoro, Richard Burns, Ian Caldas, Bryce Carson, Sam Champer, Deborah Charlesworth, Jeremy Van Cleve, Jonathan Cocker, Zuxi Cui, Jean Cury, Michael DeGiorgio, A.P. Jason de Koning, Emily Dennis, Jordan Rohmeyer Dherby, Russell Dinnage, Alan Downey-Wall, Ian Dworkin, Julia Frank, Jared Galloway, Jesse Garcia, Kimberley Gilbert, Graham Gower, Alexandre Harris, Kelley Harris, Rebecca Harris, Matthew Hartfield, Ding He, Jody Hey, Marcus Hicks, Kathryn Hodgins, Christian Huber, Melissa Jane Hubisz, Emilia Huerta-Sanchez, Chaz Hyseni, Jacob Malte Jensen, Peter Keightley, Jerome Kelleher, Andy Kern, Bhavin Khatri, Bernard Kim, Isabel Kim, Jere Koskela, Athanasios Kousathanas, Peter Krawitz, Chris Kyriazis, Benjamin Laenen, Anna Maria Langmüller, Áki Láruson, Stefan Laurent, Clancy Lawler, Anita Lerch, Mitchell Lokey, Eugenio Lopez, Kathleen Lotterhos, Nicolas Lou, Andrew Marderstein, Sebastian Matuszewski, Mikhail Matz, Rupert Mazzucco, Christopher McAllester, Maéva Mollion, Miguel Navascués, Chase Nelson, Dominic Nelson, Bruno Nevado, Tram Nguyen, Etsuko Nonaka, Boyana Norris, Nathan Oakes, Nick O'Brien, Omar Eduardo Cornejo Ordaz, Matt Osmond, Greg Owens, Josephine Paris, Harvinder Pawar, Martin Petr, Denis Pierron, Fernando Racimo, Peter Ralph, Erik Regla, David Rinker, Murillo Fernando Rodrigues, Andrew Sackman, Aaron Sams, Kieran Samuk, Sara Schaal, Derek Setter, Elissa Sorojsrisom, Onuralp Söylemez, Fabian Staubach, Stefan Strütt, Michelle Su, Anastasia Teterina, Rob Unckless, Magnus Dehli Vigeland, Nathan Villiger, Christos Vlachos, Silu Wang, Clemens L. Weiß, James Whiting, Alexander Whitwam, Aaron Wolf, Yan Wong, Yannick Wurm, Alexander Xue, Justin Yeh, and Yulin Zhang. Special thanks also to the Messer Lab, the stackoverflow community, Kevin Thornton, Ryan Hernandez, and Dmitri Petrov.



Questions!

(and SLiM stickers!)

Extra slides

How to use SLiM?

- Do **initial modeling** in SLiMgui
 - interactive model development & visual debugging
 - syntax coloring, online docs, code completion
- Do **production runs** on the cluster
 - trivial to build and run on a computing cluster
 - do many replicate runs simultaneously, one per core
- Do **post-run analysis** in Eidos, Python, or R
 - a lot of analysis can be done in-script in Eidos
 - .trees output can be read in Python with `pyslim`

WF

nonWF

The tick cycle

0. Execution of `first()` events

1. Execution of `early()` events

2. Generation of offspring:

2.1. Choose source subpop

2.2. Choose parent 1

2.3. Choose parent 2
(`mateChoice()` callbacks)

2.4. Generate the offspring
(including `mutation()` and
`recombination()` callbacks)

2.5. Suppress/modify child
(`modifyChild()` callbacks)

3. Removal of fixed mutations

4. Offspring become parents

5. Execution of `late()` events

6. Fitness value recalculation
using `fitness()` callbacks

7. Generation count increment

0. Execution of `first()` events

1. Generation of offspring:

1.1. Call `reproduction()`
callbacks for individuals

1.2. The callback(s) make
calls requesting offspring

1.3. Generate the offspring
(including `mutation()` and
`recombination()` callbacks)

1.4. Suppress/modify child
(`modifyChild()` callbacks)

2. Execution of `early()` events

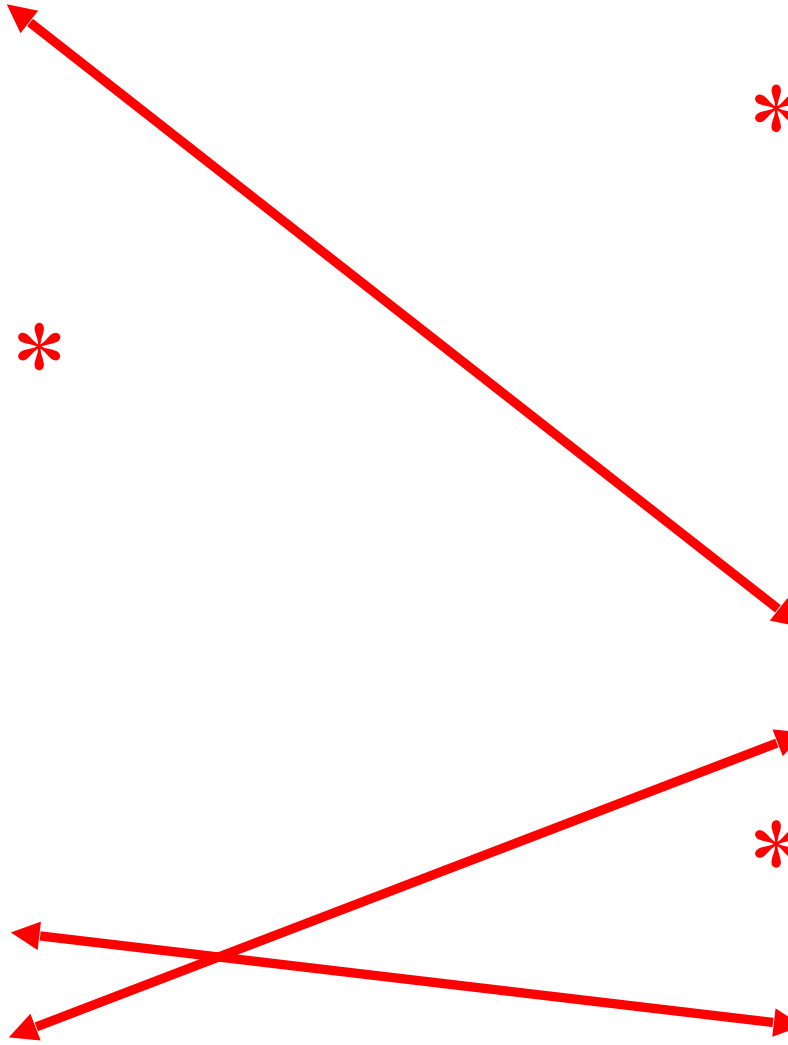
3. Fitness value recalculation
using `fitness()` callbacks

4. Selection (incl. `survival()`)

5. Removal of fixed mutations

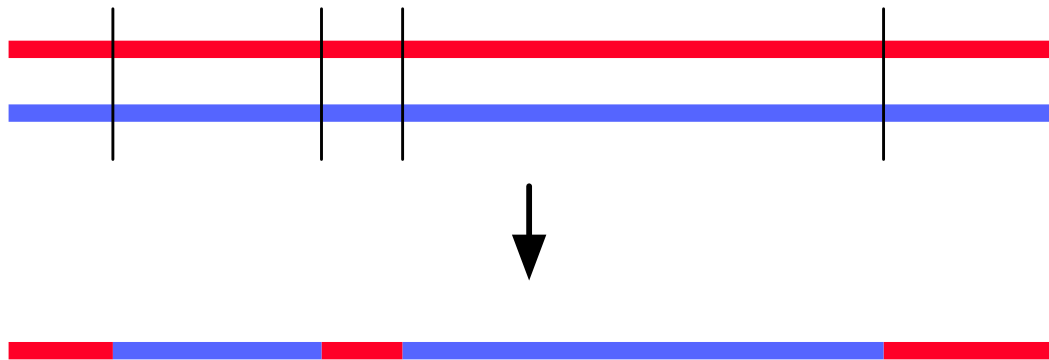
6. Execution of `late()` events

7. Generation count increment,
individual age increments



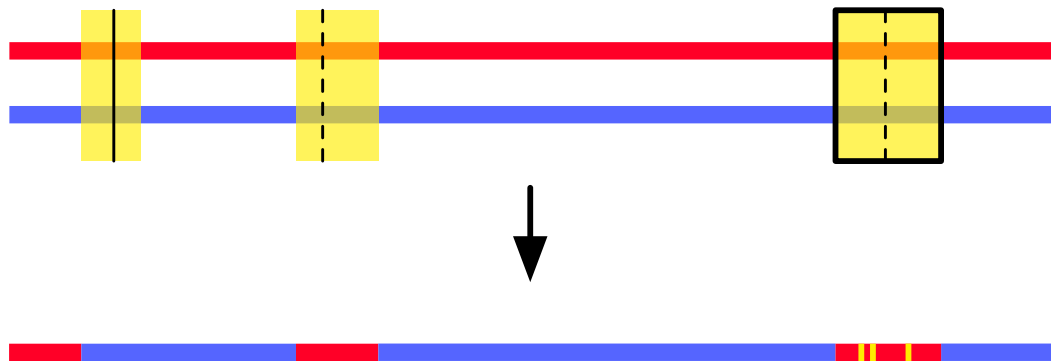
The Crossover Breakpoints Model

- During gamete generation:
 - breakpoints are drawn by probability
 - a simple crossover model is the default



The DSB Model

- Each breakpoint initiates *gene conversion*
 - DSBs can be crossovers or non-crossovers
 - gene conversion tracts can be simple or complex
 - heteroduplex mismatch repair, GC biased repair

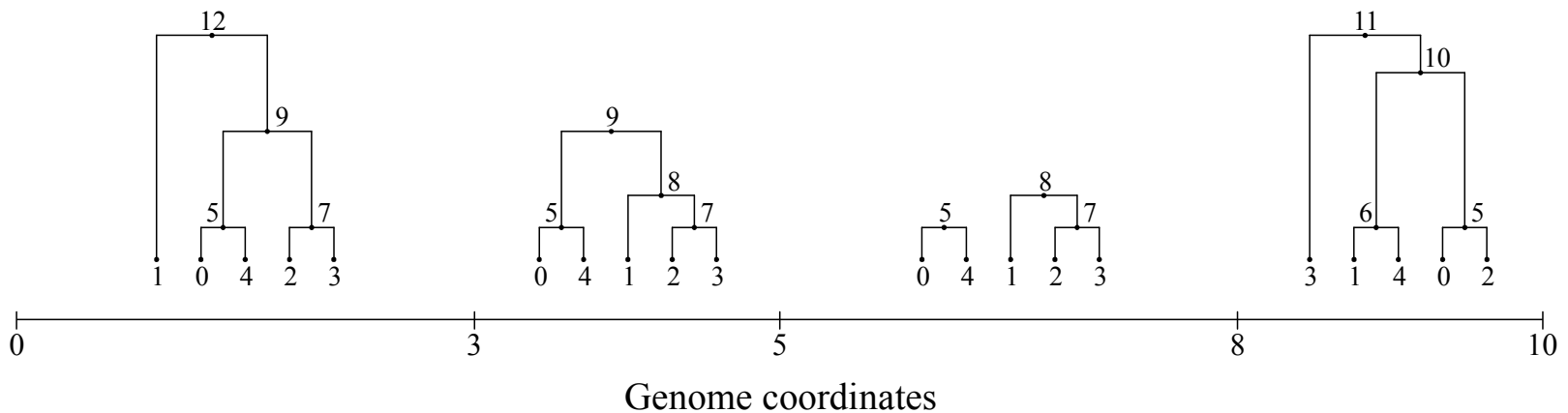


Nucleotide-based Models

- Optional facilities
 - Trinucleotide-based mutation rates
 - Reading and writing FASTA, VCF files
 - Getting the nucleotide sequence
 - Getting the codon sequence
 - Getting the amino acid sequence
 - Hotspot maps (variable mutation rate)
 - GC-biased gene conversion (gBGC)

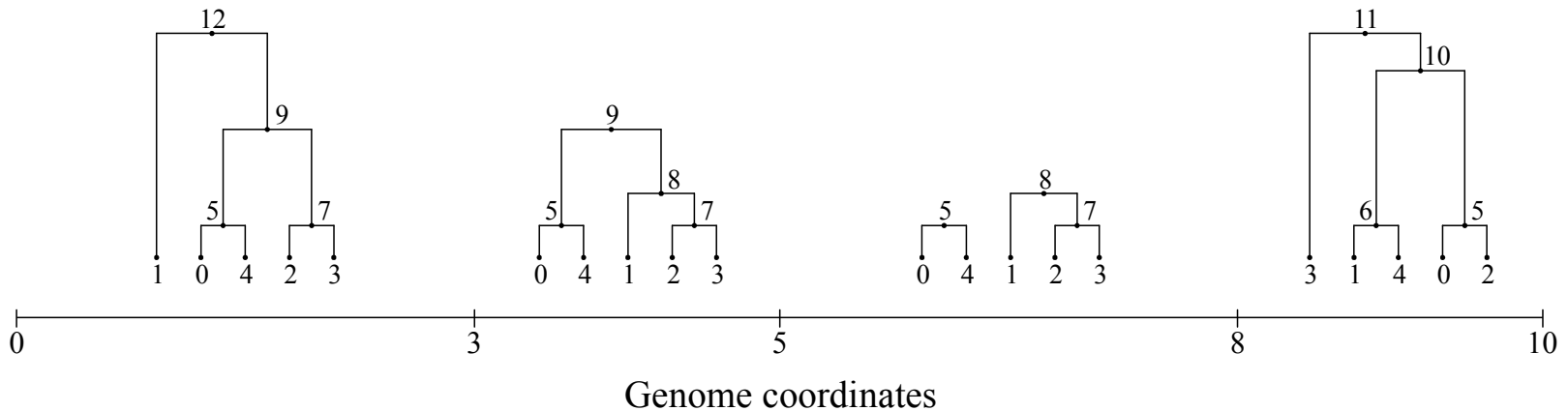
Tree sequences

- A record of the ancestry at every position
 - Originally from coalescent modeling (msprime)
 - Extremely compact due to correlations
 - Very fast to traverse and calculate statistics



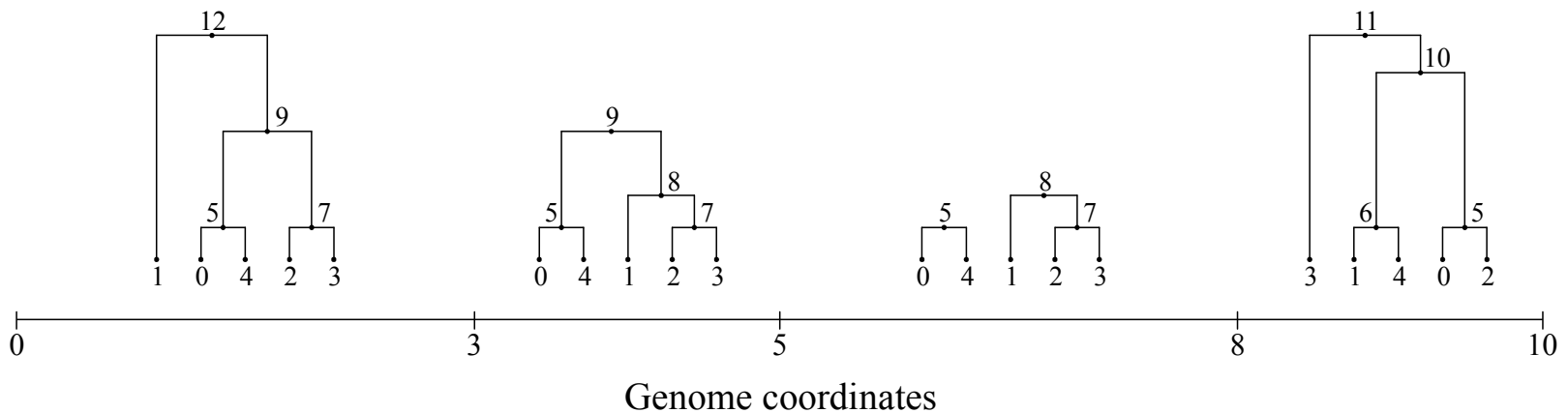
Tree sequences

- Tree sequence structure
 - Leaves are “samples” – often extant individuals
 - Internal nodes are ancestors
 - In SLiM, roots are the first generation



Tree-sequence recording

- Tracks the ancestry tree at every position
 - Neutral mutations can be overlaid after the fact
 - Neutral burn-in can be done with the coalescent
 - Recapitation can construct a coalescent history



Tree-sequence recording

- Records every new genome as a *node*
- Records every crossover as an *edge*
- Records every mutation
- This produces a huge memory footprint!
 - **Simplification** needs to be done periodically
 - Discards branches that are extinct
 - Discards intermediate nodes along branches
 - SLiM automatically simplifies periodically
 - Explicitly simplifying can improve performance

Tree-sequence recording

- Enable tree-sequence recording
 - `initializeTreeSeq()`
- Control simplification if desired
 - `simplificationRatio`, `simplificationInterval`
 - `treeSeqSimplify()`
- Remember particular individuals if desired
 - `treeSeqRememberIndividuals()`
- Output a `.trees` file at completion
 - `treeSeqOutput()`

A complete tree-seq model

```
initialize() {
  initializeTreeSeq();
  initializeMutationRate(0);
  initializeMutationType("m1", 0.5, "f", 0.0);
  initializeGenomicElementType("g1", m1, 1.0);
  initializeGenomicElement(g1, 0, 1e8-1);
  initializeRecombinationRate(1e-8);
}
1 {
  sim.addSubpop("p1", 500);
}
5000 late() {
  sim.treeSeqOutput("final.trees");
}
```

- Calls `initializeTreeSeq()` and `treeSeqOutput()`
- Uses a (neutral) mutation rate of zero

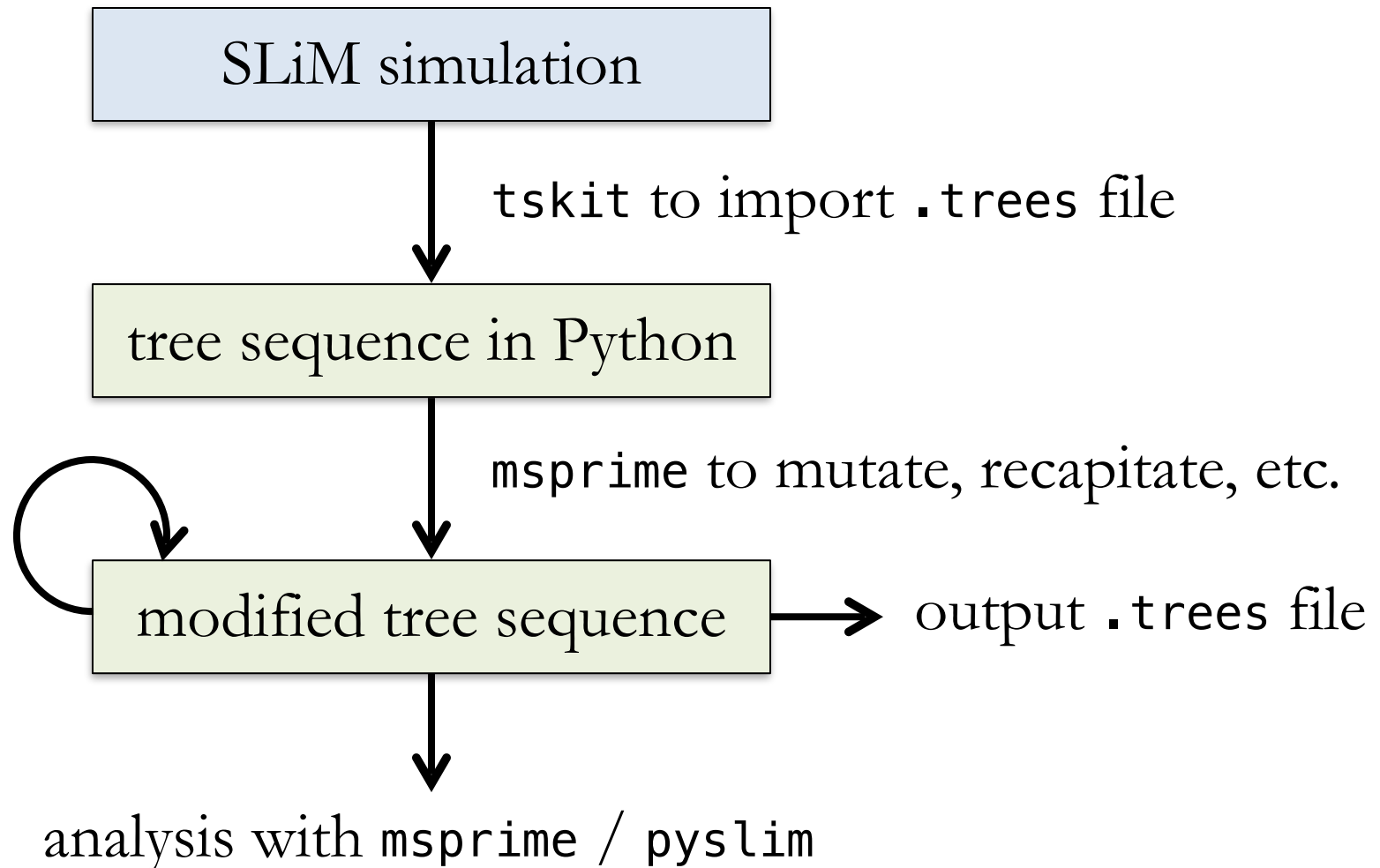
Tree-sequence analysis in Python

- `SLiM`:
 - runs forward genetic simulations
- `tskit`:
 - provides a foundation for tree sequences
- `msprime`:
 - performs mutation and coalescence
- `pyslim`:
 - knows about `SLiM .trees` files specifically

Tree-sequence analysis in Python

- Typical workflow:
 - run a simulation in SLiM and save a `.trees` file
 - read the `.trees` file from SLiM with `tskit`
 - mutate it, recapitate it, etc. with `msprime`
 - perform analyses upon it with Python
 - write out a modified `.trees` file

Tree-sequence analysis in Python



A complete Python analysis script

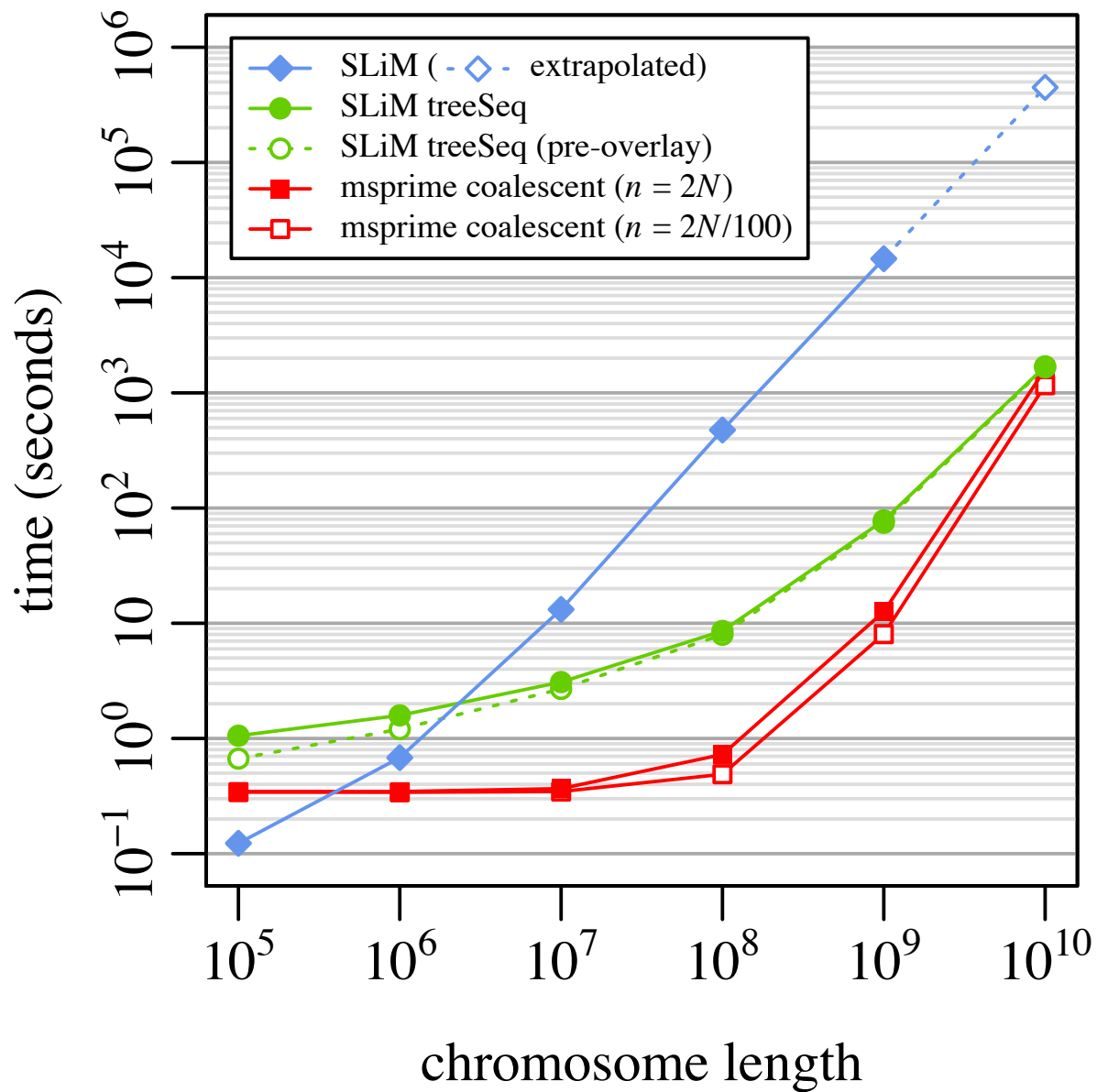
```
import msprime, tskit
```

```
ts = tskit.load("final.trees").simplify()  
mutated = msprime.mutate(ts, rate=1e-7, random_seed=1, keep=True)  
mutated.dump("final_overlaid.trees")
```

- Import msprime and tskit packages
- Load the saved .trees file with tskit
- Use msprime to overlay mutations
- Write out the new tree sequence

Tree-sequence recording

- What's the point again?
- Ancestry information is useful
- **Speed**
 - Without tree-seq, 211.9 seconds
 - With tree-seq, 4.37 seconds
 - Almost a **50×** speedup
 - Why? Neutral mutations are *overlaid*
 - Memory usage is also lower



Recapitation

- Forward simulation needs burn-in
 - provides an equilibrium initial state
- Burn-in can take a very long time!
- `msprime` can do a coalescent burn-in
- But recapitation is even better:
 - allows neutral burn-in to be skipped
 - a coalescent history is added *afterwards*
 - neutral mutations can then be overlaid
 - **even faster** than a coalescent burn-in

Resources





Received: 10 September 2018 | Revised: 6 November 2018 | Accepted: 9 November 2018

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RESOURCE ARTICLE

WILEY **MOLECULAR ECOLOGY
RESOURCES**

Tree-sequence recording in SLiM opens new horizons for forward-time simulation of whole genomes

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Philipp W. Messer^{1,*}  | Peter L. Ralph^{2,*} 

 **PLOS** | COMPUTATIONAL
BIOLOGY

RESEARCH ARTICLE

Efficient pedigree recording for fast population genetics simulation

Jerome Kelleher¹ , Kevin R. Thornton² , Jaime Ashander³ , Peter L. Ralph^{4,*} 

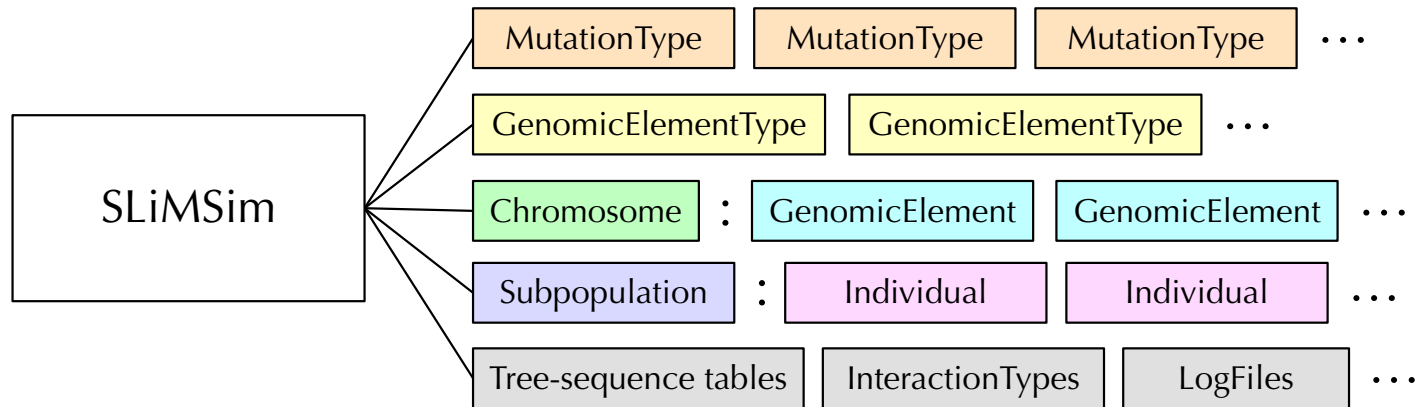
1 Big Data Institute, University of Oxford, Oxford, United Kingdom, 2 Ecology and Evolutionary Biology, University of California, Irvine, Irvine, California, United States of America, 3 Ecology and Evolutionary Biology, University of California, Los Angeles, Los Angeles, United States of America, 4 Institute for Ecology and Evolution, University of Oregon, Eugene, Oregon, United States of America

Multispecies modeling

- SLiM 4 adds support for multiple species
- Ecological interactions:
 - predation, competition, parasitism, mutualism, within-host evolution, ...
 - individual-based spatial interactions between species (local prey search, local host search, local resource competition)
- Eco-evolutionary dynamics
- Coevolutionary dynamics

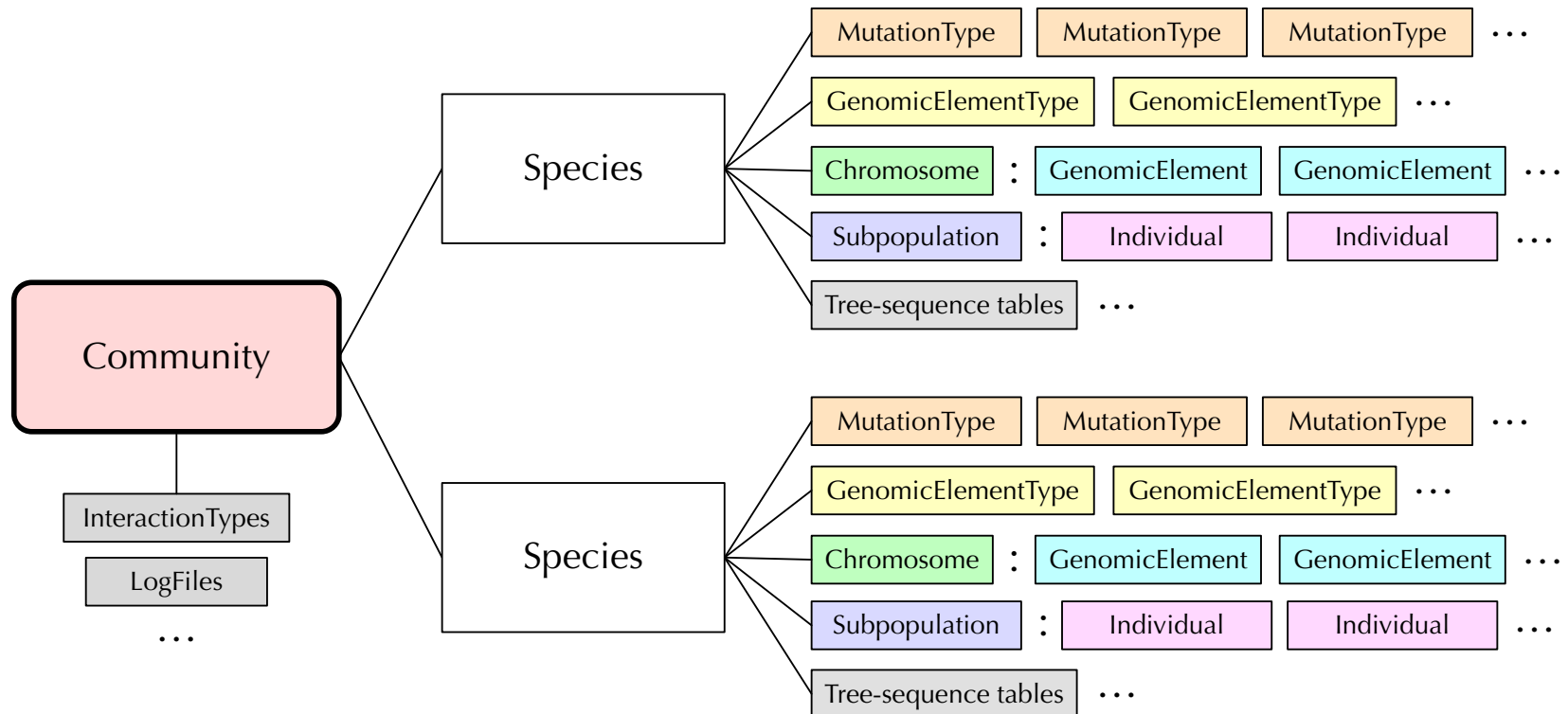
Multispecies modeling

- Now, SLiMSim represents one *simulation*:



Multispecies modeling

- In SLiM 4, SLiMSim represents one *species*:

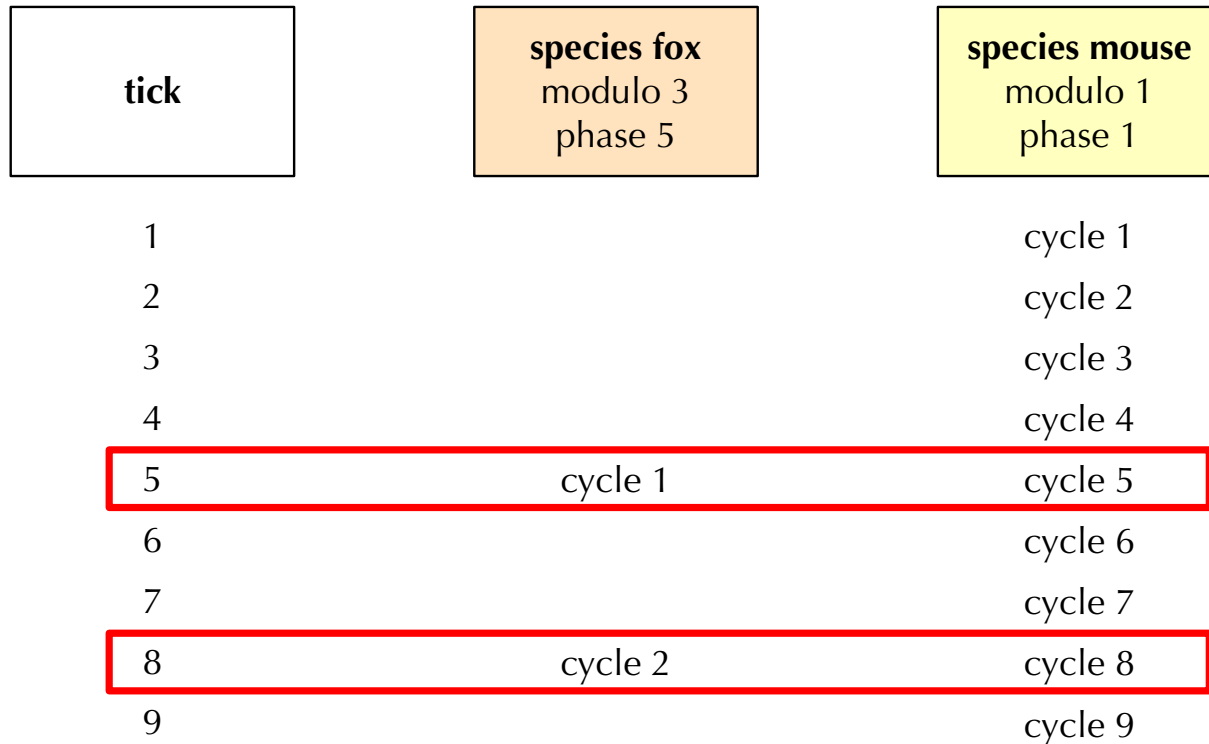


Multispecies modeling

- SLiMSim has become Species
- Community has been added on top
- Each species is independent:
 - separate genetics & behavior
 - separate scripting and callbacks
 - separate tree-sequence recording
- Separate timescales; but their execution in each tick is interleaved!

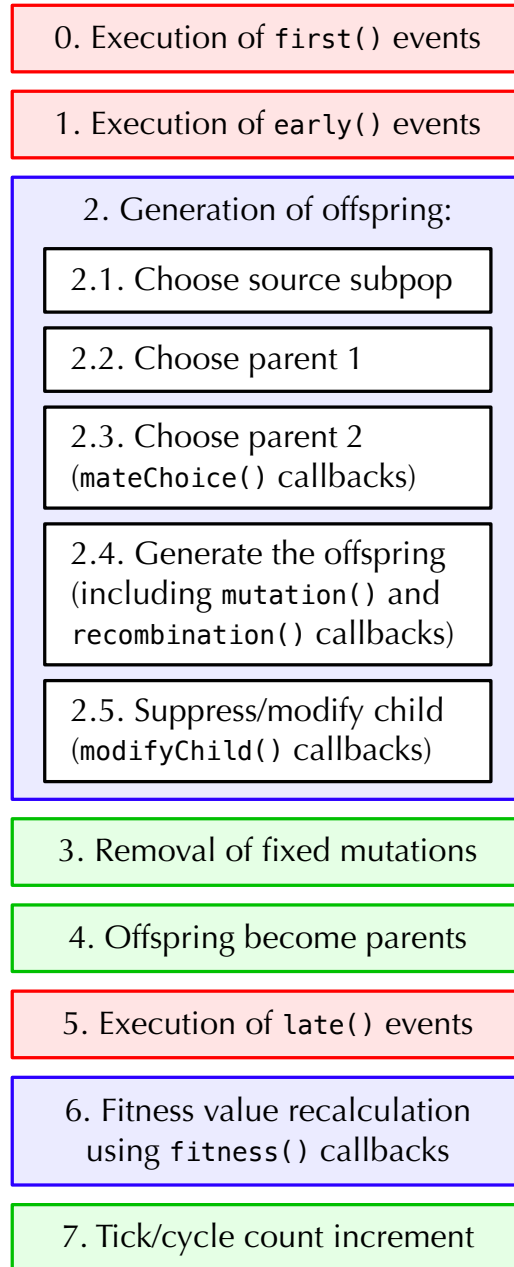
Multispecies modeling

- Time is now represented in *ticks* and *cycles*:



Intereaved tick cycles

The sequence of events within one cycle in WF models.



The sequence of events within one cycle in nonWF models.

