Module 1

Intro to Nemo

OUTLINE

- Overview of NEMO Simulation components
- User's interface: the parameter file & its syntax
- Population component
- Representation of space in Nemo
- Life cycle events (LCE)
- Traits, and their genetics
- References
- Resources

Overview of Nemo's features

Population

Spatially explicit meta-population framework Discrete space, ind. move between patches → space modeled via the migration matrix

Mating systems

Random mating/promiscuity, monogamy, polygyny, selfing, cloning, hermaphroditic, assortative

Life Cycle

Complete flexibility in the order of the events

Traits & genetics

- neutral markers (μ-satellites, SNP)
- deleterious mutations (di-allelic)
- BDM incompatibility loci
- quantitative traits: QTL with pleiotropy (*n*-traits)

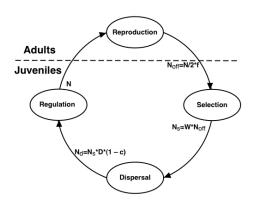
Selection

spatially & temporally varying, multi-trait fitness

Demography

stochastic, stage-structured, d.d. regulation, fitness dpdt, etc.

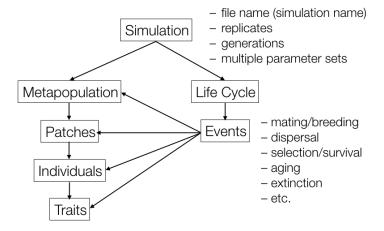
Nemo: Life Cycle



- breed
- disperse
- selection
- aging
- extinction/harvesting
- cloning
- crossing (on a pedigree)
- mutator
- stats & files I/O

Nemo Components

Simulation Components:



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Nemo: components

Simulation Components:

- Each component defines a set of parameters
- A component is included in a simulation only if its parameters are set
- Two components are mandatory: simulation and population
- A minimum of one life cycle event (LCE) is required
- Individuals without trait (no genetics) can be simulated

Nemo: components

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- Each component defines a set of parameters
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Program interface

A simple text file with the simulation's parameters and values

Nemo interface: a simple parameter file

```
## NEMO-AGE CONFIG FILE ##
## SIMULATION ##
run mode overwrite
random seed 2
root dir examples
filename example3-evolution-popini
replicates 5
generations 20000
## POPULATION ##
patch number
patch_capacity 10
### AGE STRUCTURE and LESLIE MATRIX ###
                      {{0,1,2,3,4,5}}
pop age structure
pop_transition_matrix {{0, 0, 0, 0, 0, 124}}
                       {0.83, 0, 0, 0, 0, 0}
                       {0, 0.92, 0, 0, 0, 0}
                       {0. 0. 0.93. 0. 0. 0}
                       {0, 0, 0, 0.26, 0, 0}
                       {0, 0, 0, 0, 0.43, 0.53}}
## LIFE CYCLE EVENTS ##
quanti init
breed
save stats
save files
regulation
viability_selection 5
aging multi
store
## MATING SYSTEM ##
mating system 1 #random mating
```

Syntax of the parameter file

Basic structure of the parameter file:

- ightarrow a list of parameter argument pairs, separated by at least one space
- \rightarrow each pair on a single line.

Parameter specification:

```
replicates 10 generations 100000
```

Comments:

```
# this is a one-line comment
#/ this is the start of a block comment
text within a block comment
text within a block comment
text within a block comment
/# this is the end of a block comment.
```

Syntax of the parameter file: matrix

matrix arguments: comma separated elements within curly brackets matrix_param {{row 1}{row 2}{col1, col2, col3}{m41,m42,m43}} dispersal_matrix {{0.9,0.05,0.05}{0.05,0.9,0.05}{0.05,0.05,0.9}}

Syntax of the parameter file: matrix

matrix arguments: comma separated elements within curly brackets matrix_param {{row 1}{row 2}{col1, col2, col3}{m41,m42,m43}} dispersal_matrix {{0.9,0.05,0.05}{0.05,0.9,0.05}{0.05,0.05,0.9}}

matrix arguments can be split across multiple lines:

```
dispersal_matrix {{0.9,0.05,0.05}} {0.05,0.9,0.05} {0.05,0.05,0.9}}
```

Syntax of the parameter file: types

Numbers

dispersal_rate .001 delet_mutation_rate 2.35e-7 generations 1e5

Syntax of the parameter file: types

Numbers

dispersal_rate .001 delet_mutation_rate 2.35e-7 generations 1e5

Booleans

Works on presence/absence basis: presence = TRUE, absence = FALSE. We add a parameter to select (turn-on) a feature.

delet_save_genotypes
quanti_freq_output

Syntax of the parameter file: types

Numbers

dispersal_rate .001 delet_mutation_rate 2.35e-7 generations 1e5

Booleans

Works on presence/absence basis: presence = TRUE, absence = FALSE. We add a parameter to select (turn-on) a feature.

delet_save_genotypes
quanti_freq_output

Strings (un-quoted)

filename 10pop-N1000-disp0.1-mut0002

root_dir simProjectA/model1

Syntax of the parameter file: macros

Macros are small functions that help write parameter arguments:

```
repeat: rep(x, n, each=1, sep=",")
quanti_random_genetic_map {{rep(10,5)}}
quanti_pleio_matrix {rep("{0,1}{1,0}", 3, sep="")}
results in:
quanti_random_genetic_map {{10,10,10,10,10}}
quanti_pleio_matrix {{0,1}{1,0}{0,1}{1,0}{0,1}{1,0}}
```

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results in:
quanti_random_genetic_map {{10,10,10,10,10}}
quanti_pleio_matrix {{0,1}{1,0}{0,1}{1,0}{0,1}{1,0}}
```

```
sequence: seq(from, to, by, sep=",")
quanti_genetic_map {{seq(1,50,5)}}
dispersal_rate seq(0.01,0.1,0.01,sep=" ")
results in:
quanti_genetic_map {{1,6,11,16,21,26,31,36,41,46}}
dispersal_rate 0.01 0.02 0.03 0.04 0.05 0.06 ... 0.1
```

Sequencial parameters

Nemo Interface

Running many simulations from a single file

```
## SIMULATION ##
random seed 2131454
run mode overwrite
logfile logfile.log
root_dir test
filename landscape1 m%'.3'1
replicates 10
generations 2000
## POPULATION ##
patch number 10000
patch_capacity 500
## LIFE CYCLE EVENTS ##
breed
disperse 2
aging
## DTSPFRSAL ##
dispersal model 4 # 2D lattice
dispersal rate 0.001 0.005 0.01 0.05 0.1 0.15 0.2 0.4
dispersal lattice range 1
dispersal border model 3
```

Nemo Interface

Running many simulations from a single file

```
[fred@fred test]$ nemo2.3.46 demo-test.txt
 N E M 0 2.3.46r7 [09 Feb 2017]
 Copyright (C) blablabla
 http://nemo2.sourceforge.net
reading parameters from "demo-test.txt"
setting random seed from input value: 2131454
--- SIMULATION 1/8 ---- [ landscape1 m001 ]
   start: 19-06-2017 17:40:19
   mode: overwrite
   traits:
   LCEs: breed(1), disperse(2), aging(3),
   outputs: test/{*.log}
   replicate 10/10 [17:41:50] 2000/2000
   end: 19-06-2017 17:42:01
--- done (CPU time: 00:01:41s)
--- SIMULATION 2/8 ---- [ landscape1 m005 ]
   start: 19-06-2017 17:42:01
   1...1
--- done (CPU time: 00:01:46s)
--- SIMULATION 3/8 ---- [ landscape1 m010 ]
```

Syntax of the parameter file

temporal arguments:

```
(@g0 initial_value, @g123 new_value1, @g456 new_value2)
```

Temporal arguments must be within '()', comma-separated, and start with <code>@gO</code> for initialization at the first generation.

external file argument: &path/to/file.txt

The argument value in the file must be specified with the same format as if it were provided in the parameter file itself.

line continuation: character \

Arguments can spread over multiple lines when using the 'escape' character \. Example:

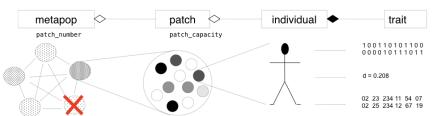
```
(@g0 initial_value, @g123 new_value1, @g456 new_value2, \ @g789 new_value3)
```

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Nemo Components

Metapopulation framework

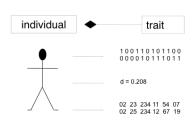
- can set the: number of patches & carrying capacities (K♀, K₺)
- patch size is dynamical: $N_t = \sum$ (stochastic events)
- extinction/colonisation events can occur
- can update the population structure (patch number & capacity)
- can set the age structure (overlapping generations)



Nemo Components

Individuals

- are diploid
- have a gender and an age
- are a collection of traits



```
Population parameters
# setting 1:
patch_number
                 128
patch_capacity
                1000
                       # will fill patches with 500 females and 500 males
#setting 2:
patch_number
                 128
patch_nbfem
                 1000 # only females if we model hermaphrodites (see mating system
patch_nbmal
                 0
#setting 3:
patch_capacity
                 \{\{10,0,23,50,1298,5,0,0,0,1000\}\}\ #patch_number = array size = 10
```

The parameter patch_capacity sets the maximum patch size, or its carrying capacity K.

```
Population parameters
# setting 1:
patch_number
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                 \{\{10,0,23,50,1298,5,0,0,0,1000\}\}\ #patch_number = array size = 10
```

The parameter patch_capacity sets the maximum patch size, or its carrying capacity K.

If set to 0, the patch will be empty after regulation (see the aging LCE).

```
Population parameters
# setting 1:
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patch_nbmal
                 0
#setting 3:
                 \{\{10,0,23,50,1298,5,0,0,0,1000\}\}\ #patch_number = array size = 10
patch_capacity
```

The parameter patch_capacity sets the maximum patch size, or its carrying capacity K.

If set to 0, the patch will be empty after regulation (see the aging LCE).

Useful when one wants to "open" the patch at a later generation with a temporal arguments.

Nemo Components

Dispersal and representation of Space

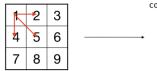
- spatially explicit, but no explicit x-y coordinates
- space abstracted into a migration matrix
- reduced (connectivity) matrices allow simulation of large landscapes

Nemo Components

Dispersal and representation of Space

- spatially explicit, but no explicit x-y coordinates
- space abstracted into a migration matrix
- reduced (connectivity) matrices allow simulation of large landscapes

patches:



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```
## Simple simulation example ##
random seed 2131454
run mode
           overwrite
logfile
          test.log
roo dir
          test
filenames landscape1 m0.005
replicates 10
generations 1000
## POPULATION ##
patch number 200
patch_capacity 500
## LIFE CYCLE EVENT ##
breed
disperse
aging
## DISPERSAL LCE ##
# dispersal models:
# 1 = Island Model Migrant Pool
# 2 = Island Model Propagule Pool
# 3 = Stepping Stone Model 1D
# 4 = Lattice Model
dispersal model 1
dispersal rate 0.005
# lattice example:
dispersal model 4
dispersal rate 0.005
dispersal lattice range 1
dispersal lattice model 3
# using dispersal matrices:
dispersal connectivity_matrix &Patch-connectivity.txt
dispersal reduced matrix &Patch-dispersal-rates.txt
```

dispersal connectivity matrix:

dispersal rate matrix:

```
{0.992589103853264, 0.00222727779649963, 0.002272779649963, 0.000884553280134066, 0.000373286982200115, 0.00289153576982218, 0.00221956896107078, 0.00221956896107078, 0.00221956896107078, 0.00088149168440329, 0.6 (0.988369866206209, 0.00221781038671654, 0.00221781038671654, 0.00221781038671654, 0.000880793274623348, 0.00281781038677, 0.00221721188901334, 0.00221721188901334, 0.00281721188901334, 0.00281721188901334, 0.00281721188901334, 0.00281721188901334, 0.0088055558399163, 0.6 (0.987994087279237, 0.00221696717362815, 0.00221696717362815, 0.002216966717362815, 0.00088048034833681, 0.6 (0.987994087279237, 0.00221696498155031, 0.00221696917362815, 0.00221696917362815, 0.00281696717362815, 0.000880451502692947, 0.006 (0.987986351609929, 0.0022169498155031, 0.0022169498155031, 0.002880451502692947, 0.006 (0.987986351609929, 0.0022169498155031, 0.0022169498155031, 0.002808451502692947, 0.006 (0.987986351609929, 0.0022169498155031, 0.0022169498155031, 0.002808451502692947, 0.006 (0.987986351609929, 0.0022169498155031, 0.0022169498155031, 0.000880451502692947, 0.006 (0.987986351609929, 0.0022169498155031, 0.0022169498155031, 0.000880451502692947, 0.006 (0.987986351609929, 0.0022169498155031, 0.0022169498155031, 0.000880451502692947, 0.006 (0.987986351609929, 0.0022169498155031, 0.0022169498155031, 0.000880451502692947, 0.006 (0.987986351609929, 0.0022169498155031, 0.0022169498155031, 0.000880451502692947, 0.006 (0.987986351609929, 0.0022169498155031, 0.0022169498155031, 0.0022169498155031, 0.000880451502692947, 0.006
```

Nemo Components

Life-cycle events:

aging: increase the age of the individuals, perform patch regulation breed: mate and breed, create new offspring generation breed_wolbachia: breed and Wolbachia transmission/infection cross: perform a half-sib, full-sib mating design (NCI) disperse: offspring dispersal disperse_evoldisp: offspring dispersal with evolving dispersal rates extinction: random patch extinction or harvesting regulation: patch regulation (to carrying capacity) resize: modify population size (patch number and/or size) save_files: write output files to disk save_stats: record statistics store: save simulation data to binary files selection: perform viability selection on the offspring generation breed_disperse: breed with backward migration (Wright-Fisher model) breed_selection: breed with selection (faster) breed_selection_disperse: all in one (Wright-Fisher with selection)

Nemo Components

Life-cycle events:

→ effect on population composition:

LCE	Offspring	Adults
aging	move to adults	_
breed	+	required
cross	+	required
disperse	x (required)	
extinction	X	Х
regulation	X	Х
resize	X	Х
selection	x (required)	

Table 4.1 in Nemo-manual p.33

Ordering of the LCEs

The LCEs can be set in *almost* any order in the life cycle. Some dependencies exist because the LCEs change the content of the age classes.

This works breed 1 # adds offspring viability_selection 2 disperse 3 aging 4 #removes offspring

This doesn't works	
breed	1
aging	2 #removes offspring
viability_selection	3 #no offspring
disperse	4 #no offspring

This works too		
breed	1	
disperse	2	
viability_selection	3	# in arrival patch
aging	4	-

Ordering of the LCEs

The LCEs can be set in *almost* any order in the life cycle. Some dependencies exist because the LCEs change the content of the age classes.

This works breed 1 # adds offspring viability_selection 2 disperse 3 aging 4 #removes offspring

-	This doesn't works	
g	breed aging viability_selection disperse	1 2 #removes offspring 3 #no offspring 4 #no offspring

which is a first or a second control of

This works too breed 1 disperse 2 viability_selection 3 # in arrival patch aging 4

The minimum life cycle		
breed	1	
aging	2	

Ordering of the LCEs

The LCEs can be set in *almost* any order in the life cycle. Some dependencies exist because the LCEs change the content of the age classes.

This works

breed viability_selection	1 # adds offspring
disperse	3
aging	4 #removes offspring

This doesn't works

breed	1
aging	2 #removes offspring
viability_selection	3 #no offspring
disperse	4 #no offspring

This works too

breed	1	
disperse	2	
viability_selection	3	# in arrival patch
aging	4	

The minimum life cycle

breed	1	
aging	2	

This one is fine too!

```
patch_number 1
patch_capacity 100
source_pop path/to/sim-P1-N100.bin
## life cycle :
save_stats 1
save_files 2
```

Nemo Components

Traits:

sequence-based traits

ntrl : neutral markers (microsat, SNP)

delet : deleterious mutations (biallelic loci)

quanti: quantitative trait loci (continous, biallelic)dmi : Dobzhanski-Muller incompatibility loci

disp : dispersal locus (evolving dispersal rates)

wolb : Wolbachia infection status (endosymbiont with CI)

BUT, traits are optional, individuals may not carry any trait

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Neutral trait ntrl

```
## NEUTRAL MARKER TRAIT ##
# 1. microsatellites
ntrl loci
                        25
ntrl all
                        256
ntrl_mutation_model
                              #1: single-step mutation, 2: k-allele model
ntrl mutation rate
                        0.001
ntrl recombination rate 0.5
ntrl_save_genotype
                        FSTAT
ntrl save freq
                        locus
ntrl_output_dir
                        ntrl
ntrl_output_logtime
                        {{1,50,1000}}
```

Neutral trait ntrl

```
## NEUTRAL MARKER TRAIT ##
# 1. microsatellites
ntrl loci
                        25
ntrl all
                        256
ntrl mutation model
                               #1: single-step mutation, 2: k-allele model
ntrl mutation rate
                        0.001
ntrl recombination rate 0.5
ntrl save genotype
                        FSTAT
ntrl save freq
                        locus
ntrl output dir
                        ntrl
ntrl_output_logtime
                        {{1,50,1000}}
```

Deleterious mutations trait delet

```
## DELET TRAIT ##
delet loci
                           10000
delet_init_freq
delet mutation rate
                           1e-5
delet_backmutation_rate
                           1e-7
delet_fitness_model
                                     # multiplicative across loci
delet effects mean
                           0.05
                                     # mean (negative) fitness effect, s
delet dominance mean
                           0.36
                                     # mean of the distribution of h
delet effects distribution lognormal # the DFE
delet effects dist param1
                           -6.4
delet effects dist param2
                           5.3
delet save genotype
```

Quantitative traits quant

```
## OUANT TRAIT ##
# 1. Gaussian additive model:
quanti traits
quanti loci
                         50
                                     # additive loci
quanti allele model
                         continuous # mutations drawn from a normal distribution
quanti mutation variance 0.05
                                     # a^2; variance of the normal distribution
quanti mutation rate
                                     # thus Vm = 2L\mu a^2 = 0.0005
                         0.0001
quanti_recombination_rate 0.5
                                     # default
quanti init value
                                     # initial trait phenotypic value is 0
quanti init model
                                     # random mutations added
quanti environmental variance 0.1 # to set heritability < 1
```

Quantitative traits quant

```
## OUANT TRAIT ##
# 1. Gaussian additive model:
quanti traits
quanti loci
                                       # additive loci
                          50
quanti allele model
                          continuous # mutations drawn from a normal distribution
quanti mutation variance
                                       # a^2; variance of the normal distribution
                          0.05
quanti mutation rate
                          0.0001
                                       # thus Vm = 2L\mu a^2 = 0.0005
quanti recombination rate 0.5
                                       # default
quanti init value
                                      # initial trait phenotypic value is 0
quanti init model
                                      # random mutations added
quanti environmental variance 0.1
                                      # to set heritability < 1
```

```
# 2. Discrete di-allelic model:
quanti traits
quanti loci
                          500
                                       # additive loci
quanti allele model
                          diallelic HC # only 2 allele are segregating +a/-a
quanti_allele_value
                          0.01
                                       # phenotypic range is [-10, +10], by step of 0.01
quanti_mutation_rate
                          0.0001
                                       # switches between +a/-a states
quanti recombination rate {{1e-5}{1e-5}{1e-5}{1e-5}} # 5 chromosomes
quanti init model
                                       # each locus is alternatively homozygote +a or -a
quanti output
                          PLINK
                                       # PLINK .ped, .fam, .map files
```

Pleiotropic traits with quant

```
# 3. Pleiotropy in the genotype-phenotype map
quanti traits
                                      # three phenotypic traits are modeled
quanti loci
                        100
                                     # loci fully pleiotropic, effect on all traits
quanti_allele_model
                                      # mandatory for pleiotropic level > 2
                        continuous
quanti mutation rate
                        0.001
quanti mutation matrix
                        {{0.05, 0, 0.025} # multivariate Gaussian distribution
                         {0, 0.05, 0.0125} #mutations have correlated effects on
                         {0.025, 0.0125, 0.05}} #traits 1&3 (0.5) and 2&3 (0.25)
quanti init model
```

Variable pleiotropy in the GP map with quant



Jobran Chebib

Availabale in nemo2.4.0!!!

Puting components together

```
## Simple simulation example ##
random seed 2131454
run mode
           overwrite
logfile
            test.log
root_dir
           test
filename landscape1_m0.005
replicates 10
generations 1008
## POPULATION ##
patch number
                     208
patch capacity
                     500
## LIFE CYCLE EVENT ##
breed
disperse
vlability_selection
aging
## DISPERSAL LCE ##
dispersal model
                           # island model
dispersal rate
                     0.005
## BREED LCE ##
mating system
mean_fecundity
## SELECTION LCE ##
selection trait
                       quant
selection model
                       gausstan
selection_trait_dimension 1
selection variance
selection_local_optima {{0}{1}{2}{3}{4}{5}} # recycled across patches
## TRAITS ##
# NTRL
ntrl loci
                       100000
ntrl_all
ntrl mutation model
ntrl mutation rate
                       1e-6
ntrl_random_genetic_map {{10}{10}{10}{10}} # 5 linkage groups, 10cM each
ntrl genetic map resolution 0.001 #ie 10/10000: 10000 sites available per chromosome
# OUANTI
quanti traits
quanti loci
                                      # additive loci
quanti allele model
                         diallelic HC # only 2 allele are segregating: +a/-a
quanti allele value
                         0.01
                                      # phenotypic range is [-10, +10], by step of 0.01
quanti mutation rate
                         0.0801
                                      # switches between +a/-a states
quanti recombination rate {{1e-5}{1e-5}{1e-5}{1e-5}} # 5 chromosomes
quanti_init_model
                                      # each locus is alternatively homozygote +a or -a
quanti output
                         PLINK
                                      # PLINK .ped. .fam. .map files
```

Other features

- Store and reload: use store LCE to save and load binary files
- Stage-structured populations: NEMO-AGE
- Multi-species simulations: in development
- Submit jobs on a cluster from an input file: NEMOSUB
- Parallelization: using MPI version to run replicates in parallel on a cluster

nemosub

nemosub: submitting simulations to a job scheduler

```
## job scheduling parameters ## <-- nemosub
sub program sbatch
sub script directive SBATCH
sub parameters -mem-per-cpu=16000
sub script args nemo3.0.16
sub iobname camp%'.4'2g%1s%3
## dummy sequence parameters
## NEMO PARAMS ##
filename campanula mut%'.4'2 g%1 s%3 VS50
## SOURCE POP ##
source_pop campanula_mut%'.4'2_g%1 VS50
source_preserve
[...]
## POPULATION ##
patch number 1024
patch_nbfem (@g0 &init_K_campanula_%1.txt, @g1 1000)
## RATE ENV CHANGE ##
rate environmental change (@q0 &nochange.txt, @q10 &rate 2020 s%3 %1.txt, @q21
&rate 2030 s%3 %1.txt, @g31 &rate 2040 s%3 %1.txt, @g41 [...] )
```

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[fred@fred test]\$ nemosub env-change.txt

Nemo: what have we done with it?

- Architecture of adaptive phenotypic divergence

 Yeaman & Guillaume 2009 (Evolution); Yeaman & Whitlock 2011 (Evolution); Débarre et al. 2015 (Am Nat);

 Yeaman 2015 (Am Nat); with phenotypic plasticity: Schmidt & Guillaume 2017 (Heredity)
- Multivariate quantitative genetics models with pleiotropy
 Guillaume & Whitlock 2007 (Evolution); Guillaume 2011 (Evolution); Guillaume & Otto 2012 (Genetics); Chebib
 & Guillaume 2017, 2021 (Evolution, Genetics)
- Eco-Evolutionary dynamics in heterogeneous environments
 species' range evolution: Gilbert et al. 2017 (Am Nat); Cotto et al. 2017 (Nat Comm); Postuma et al. 2020 (Ecosphere) with phenotypic plasticity: Schmidt et al. 2019 (Am Nat)
- Reconstructing patterns of genetic variation from demographic scenarios Dynamics of deleterious mutations during recolonization: Grossen et al. 2020 (Nat Comm); Adaptive variation for genomic vulnerability analysis: Dauphin et al. 2021 (Glob Change Biol)
- Multi-species eco-evo dynamics in changing environments

 Species competition in space and time: Gidoin et al. in prep

Resources

Nemo:

- homepage: https://nemo2.sourceforge.io
- info: NemoSimul@twitter; https://groups.google.com/g/nemo-announce
- support & discussion: https://groups.google.com/g/nemo-simul
- Nemo-age (stage-structured version): https://bitbucket.org/ecoevo/nemo-age-release

Papers:

Guillaume, F. and Rougemont, J. (2006) **Nemo:** an evolutionary and population genetics programming framework. *Bioinformatics* 22:2556-2557

Cotto, O., Schmid, M. and Guillaume, F. (2020) **Nemo-age: spatially explicit simulations of eco-evolutionary dynamics in stage-structured populations under changing environments.** *Methods in Ecology and Evolution* 11:1227-1236

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Syntax of the parameter file: macros

Dealing with argument strings:

In example $rep("{0,1}{1,0}", 3, sep="")$, we added quotes " "to enclose the first argument to rep().

- ⇒ Arguments to a macro must be quoted when they include *delimiters* (commas ',') or *enclosers* (parentheses: '()', '{}').
- ⇒ This is required to not interpret within-string elements as separate arguments to the macro.

Macros can be nested:

Example: rep(seq(1,5,1), 2), but this will not work! Nemo will return:

```
***ERROR*** macro "rep" can have max 4 arguments: rep(x, n, each=1, sep=",")
```

This error is issued because rep was called as: rep(1,2,3,4,5, 2).

 \Rightarrow Result of seq(1,5,1) must be quoted with macro q():

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 \Rightarrow the call to rep becomes: rep("1,2,3,4,5",2)