

# Macro-evolution model

The script is available at : [https://github.com/DominiqueGravel/ms\\_diversification](https://github.com/DominiqueGravel/ms_diversification) (code folder) and in the dopbox *Macroevo\_Interaction* (same folder)

The aim of the model is to recreate establishment/extinction events in a community of a particular type of interactions (*i.e.* facilitation, competition or predator-prey). It allows us to access the structure of the species interactions network over time, and to build the phylogenetic tree of the community.

:warning: Here we are talking about **unipartite** networks.

## Model functioning

Before running the model, we have to indicate :

- the number of time steps (*nsteps*),
- the seed,
- a set of parameters (defined at the end of the document)

## Before all : Prepare tables and the first species

Setting tables *traits<sub>mat</sub>*, *anc*, *extinction* and *pres*.

The aim here is to build empty tables and matrices, which will be filled all along the simulation.

- *traits<sub>mat</sub>* table compiles all the traits combinations of established species. The traits of interest here (for competition and facilitation) are the traits *n* (niche optimum) and *r* (half of niche range).

Trait n	Trait r	Trait o
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- *anc* compiles the time step at which a species establish into the community and its ancestor.

time step	ancestor	new species
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- *extinction* compiles the species extinctions and the time step at with the extinction occurs.

time step	extinct species
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- *pres* compiles all the present species in the community at a time  $t$ . Each column is a species and each row a time step. *pres* is pre-build with  $S_{max}$  columns and  $nsteps$  row. It is a binary matrix where 1 means the species is present and 0 absent.

	Species1	Species2	Species3	...
time 1				
time 2				
...				

Each species is represented by a number going from 1 to  $S_{max}$ , attributed by arrival order.

### Setting the first species

To start the simulation, a first species is generated using the function `rand_traits_anc`. Its traits ( $n$  and  $o$ ) are randomly selected into a uniform distribution between 0 and 1, and  $r$  is fixed by the parameter  $av_r$ .

Then the number of species,  $S$ , in the community is setted to 1 (as we have only one species for now).

**Now that the model is ready to really start, the two later parts of the model (establishment and extinction) will be executed at each time step, as part as a loop, as long as  $S_{max}$  or  $nsteps$  has been reached.**

### Inside the loop, First step : See if new species can establish

The first thing is to check the total number of species in the community (not only the actual number of species at the time  $t$ ). If the limit  $S_{max}$  has been reached, the model stops.

For each present species, a random number is picked on a uniform distribution between 0 and 1. Mutation is allowed if this number is below the threshold of the mutation probability ( $u_{max}$ ), defined by

$$P(mutation) = \frac{u_{max}}{(1 + e^{(d * (S_t - I_{max}))})},$$

where  $u_{max}$  is ,  $d$  a constant,  $S$  species number at  $t$  time/step and  $I_{max}$  the maximal number of species in the community.

### Mutation allowed? Yes!

A *mutant* trait  $n_m$  is picked on a normal distribution (Fig. 1) where the ancestor trait  $n$  is the mean, and the standard deviation is defined by a number higher than the total interaction range.

$$P(n_m) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{(n_m - n)^2}{2\sigma^2}}$$

,

$$\sigma = 2 * av_r + \epsilon$$

.

A new value for the trait  $o$  ( $o_m$ ) is recorded as the value of  $n$ . The trait  $r$  is also subject to mutation. The niche range of the new species ,  $r_m$  is defined based on  $r$  plus a number picked on a normal distribution of mean 0 and standard deviation of 0,2.

Once the *mutant* traits have been setted, we calculate the number of possible interaction this *mutant* species can have. First, the function `get_L_vec`, calculate the number of species with a trait  $n$  within the range of  $[n_m - r_m, n_m + r_m]$  of the *mutant* species.

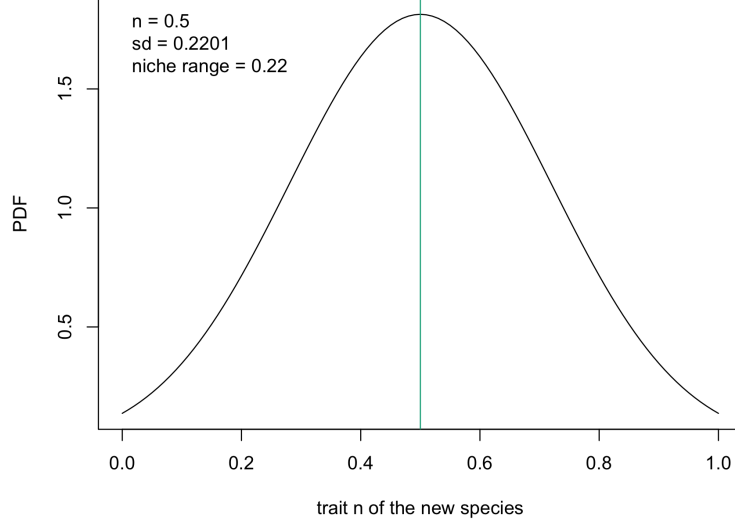


Figure 1: Examples of normal distribution used to generate the trait  $n$  of a new species.

Then, we test for establishment the *mutant* species. The probability of establishment is different depending on the interaction type. For facilitation interactions (Fig. 2), the probability follows:

$$P(\text{establishment}_f) = u_0 + u_1 \cdot e^{-a_u \cdot I_m},$$

where  $u_0$  represents the asymptotic establishment probability with infinite interactions,  $u_1$  ( $u_1 = -u_0$  for facilitation interactions) is the establishment probability with absence of interactions,  $a_u$  is the shape of the exponential decay of the colonization-interaction relationship and  $I_m$  is the sum of the possible interactions of mutant species with the rest of the community.

$I_m$  is obtained by:

$$I_m = \sum (I \cdot P) + \text{basal}_{\text{estab}},$$

where  $I$  is a vector obtained with the function `get_L_vec`,  $P$  is the species present at the time  $t$  (from *pres*) and  $\text{basal}_{\text{estab}}$  is the minimal number of basal species needed for the community not to collapse.

When simulating competition interactions (Fig. 3), the probability follows:

$$P(\text{establishment}_c) = u_{0\text{neg}} + u_{1\text{neg}} \cdot e^{-a_{\text{neg}} \cdot I_m},$$

Once the probability of establishment of the *mutant* species has been calculated, a random number is picked on a uniform distribution between 0 and 1. If this random number is lower than the probability of establishment, the *mutant* species can establish into the community.

### Establishment allowed? Yes!

If establishment is allowed, the traits of new species are recorded into the  $\text{traits}_{\text{mat}}$ , the time of arrival and related ancestor are recorded into  $\text{anc}$ , the presence of the species is recorded into *pres* at the row  $t$ , and the number of species  $S$  is increased by 1.

## Inside the loop, Second step : See if the existing species goes extinct

Once every species of the community have been checked for speciation/establishment, we test yet for extinctions.

First, we want to know which species co-occurs and interacts with which. To do so, we start by creating a co-occurrences matrix (*cooc*) between present species at the time  $t$ . Then, thanks to the function `get_L_mat`, the potential interactions matrix ( $L_p$ ) between every species in the community is calculated. Species  $i$  interacts with species  $j$  if  $n - j$  is within  $[n_i - r_i, n_i + r_i]$ . And because no self-interaction is allowed, the diagonal will always be 0. The realized interaction matrix is obtained by multiplying  $L_p$  and *cooc*.

### Extinction probability

- In case of facilitation interaction

First, the sum of the realized interaction per species is calculated by

$$I_m = \sum I + basal_{ext},$$

where  $I$  is the realized interaction per species, and  $basal_{ext}$  is the minimal number of basal species needed for the community not to collapse to fast.  $I_m$  is the vector containing the sum of species interactions per species.

Then the extinction probability (Fig. 2) is defined as :

$$P(extinction) = e_{0pos} + e_{1pos} \cdot e^{-a_{epos} \cdot I_m},$$

where  $e_{0pos}$  is the asymptotic extinction probability with infinite positive interactions,  $e_{1pos}$  is  $(1 - e_{0pos})$ ,  $a_{epos}$  is the shape of the exponential decay of the positive extinction-interaction relationship and  $I$  is the total number of interaction per species.

$P(extinction)$  is a vector containing all the probability of extinction per species.

- In case of competition interaction

Same thing than for facilitation interactions, the sum of the realized interaction per species  $I_m$  is calculated. Then the extinction probability (Fig. 3) is defined as :

$$P(extinction) = e_{0neg} \cdot (1 - e^{-a_{eneg} \cdot I_m}),$$

where  $e_{0neg}$  is the asymptotic extinction probability with infinite negative interactions,  $a_{eneg}$  is the shape of the exponential decay of the positive extinction-interaction relationship and  $I_m$  is a vector with the total number of interaction per species.

### Extinction allowed?

For an extinction to occur, a random number is picked, into a uniform distribution between 0 and 1, for every species. The extinction probability is compared to each random number. If a number is smaller than the extinction probability, the related species goes extinct.

For every species  $i$  that goes extinct, the extinction is recorded into *ext*, with the species number  $i$  and the time step  $t$  ; and *pres* is updated, replacing *pres*[ $t, i$ ] by 0.

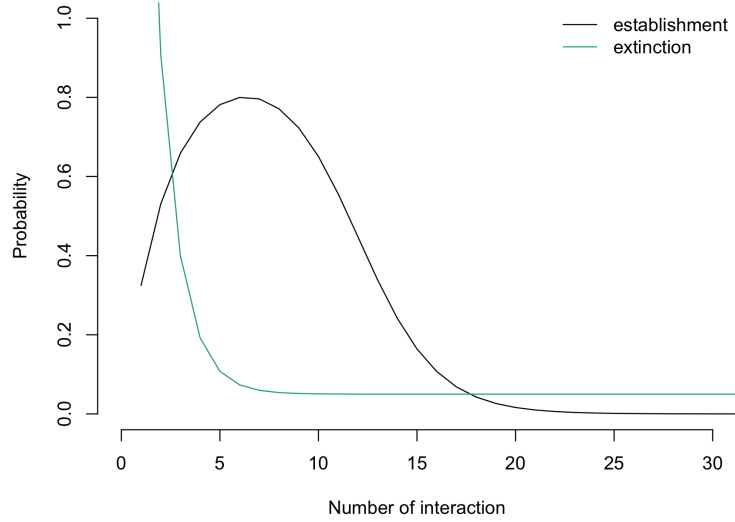


Figure 2: Example of establishment and extinction probabilities for facilitation interactions. establishment parameters :  $u_0 = 0.9$ ,  $u_1 = 0.9$ ,  $a = 0.45$ ,  $d = 0.5$ ,  $I_{\max} = 12$  ; extinction parameters :  $e_{0\text{pos}} = 0.05$ ,  $e_{1\text{pos}} = 5.19$ ,  $a_{\text{pos}} = 0.9$ ,  $I_{\max} = 12$ .

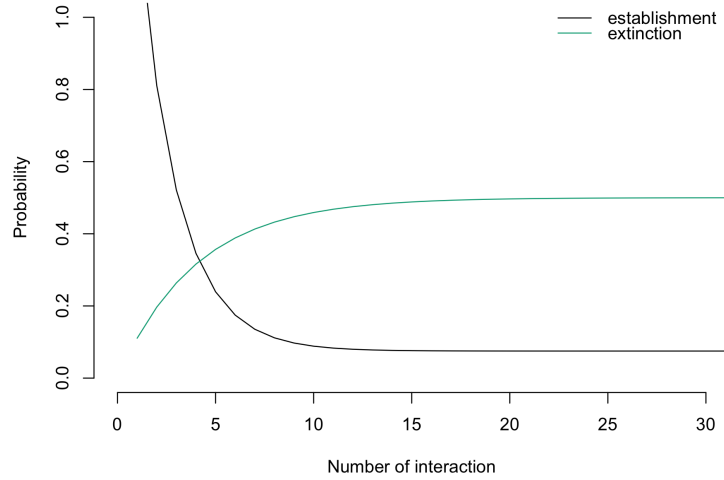


Figure 3: Example of establishment and extinction probabilities for competition interactions. establishment parameters :  $u_0 = 0.075$ ,  $u_1 = 2$ ,  $a = 0.5$  ; extinction parameters :  $e_{0\text{neg}} = 0.15$ ,  $e_{1\text{neg}} = -0.15$ ,  $a_{\text{neg}} = 0.025$ .

### Network properties

To avoid recording every interaction matrix, we calculate the network connectance and each species degree (number of interaction per species).

Because we have a undirected unipartite network where self-interactions are not allowed, the connectance is given by

$$Co = L/S^{(S-1)/2},$$

where  $L$  is the number of links and  $S$  is the number of species in the network.

## Model output

The model output gives you access to :

- *traits<sub>mat</sub>* table,
- *anc* table,
- *extinction* table,
- *pres* matrix,
- *L*, the realized interactions matrix from the last time step.

## Parameters

$u_{max}$  : Mutation probability (asymptotic establishment rate)

$u_0$  : Asymptotic establishment probability with infinite facilitation interactions

$u_1$  : Establishment probability with absence of facilitation interactions

$a_u$  : Shape of the exponential increase of the colonization - interaction relationship (facilitation)

$u_{0neg}$  : Asymptotic establishment probability with infinite competition interactions

$u_{1neg}$  : Establishment probability with absence of competition interactions

$a_{uneg}$  : Shape of the exponential decay of the colonization - interaction relationship (competition)

$e_{0neg}$  : Asymptotic extinction probability with infinite negative interactions

$e_{1neg}$  : Extinction probability with absence of interactions ( $-pars\$e_{0neg}$ )

$e_{0pos}$  : Asymptotic extinction probability with infinite positive interactions

$e_{1pos}$  : ( $1 - pars\$e_{0pos}$ )

:warning:  $u_1 - u_0$  and  $e_1 - e_0$  are the establishment and extinction rates in absence of interactions.

$a_{eneg}$  : Shape of the exponential decay of the negative extinction - interaction relationship

$a_{epos}$  : Shape of the exponential decay of the positive extinction - interaction relationship

$av_r$  : Range of the niche

$sd$  : standard deviation of the normal distribution used to calculate the trait n of a new species

$int$  : Interaction type (0 for competition, 1 for mutualism, 2 for predation)  $Bspe$  : Number of basal species needed for establishment  $Bext$  : Number of basal species needed for extinction  $Smax$  : Maximal number of species allowed during the simulation

$d$  : Shape of the exponential decay of the probability of establishment/speciation  $I_{max}$  : Maximal number of species in the community/system