A description of the Mast seeding model following the ODD protocol

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We present here a description of the mast model, following the ODD protocol (Grimm et al. 2010). The model is developed in NetLogo 5.0.1 (Wilensky 1999).

1 Purpose

Purpose of the model is to perform a "virtual experiment" to test the *predator satiation hypothesis*, advanced in literature to explain the masting phenomenon.

Masting (or mast seeding) can be defined as the synchronous production of large amounts of seeds at long intervals of time by a plant population (Janzen 1976) and it is observed in several genera. According to predator satiation hypothesis, plants would have evolved this synchronization ability to keep in check seed predators: large crops satiate seed predators that consequently destroy only a lower proportion of seeds (Silvertown 1980).

We developed a model reproducing the interactions between trees, seeds and seed predators simulating two forests: a realistic forest, where the masting phenomenon occurs, and an imaginary control one, without it. Such a comparison, that would have been impossible in the field,allows a check of the validity of the predator satiation mechanism and, more generally, a comprehensive exploration of the effects of masting on both tree and seed predator populations.

2 Entities, state variables, and scales

- The model includes three kinds of entities: patches, trees and mice. Even if the model is designed to represent a general masting situation, it is largely inspired by the empirical case presented in Wolff (1996). For illustration purposes, trees can be regarded as oaks (e.g., *Quercus rubra* and *Q. alba*), seeds as acorns and mice (namely the seed predators) as *Peromyscus maniculata*, *P. leucopus* and *Tamias striatus*.
- A time step (tick) represents a month and simulations run for 2000 months.
- The model space represents a forest; each patch is either empty or occupied by a single tree. Being the crown radius of an mature oak around 10 meters, each patch represents a land surfaces of about 300 m^2. Table 1 presents the entity attributes, while Table 2 lists the global (environmental) variables used in the model.

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Entity	Attribute	Description
Patch	*tree*?	boolean variable indicating whether the patch is occupied by a tree ($tree? = TRUE$) or empty ($tree? = FALSE$)
	seeds	variable indicating how many seeds there are within the patch (it is not necessary an integer)
Mouse	*energy*	number ≥ 0, indicating the energy stored in a mouse at the current month
	age	integer number indicating the mouse age in months
Tree	*age*	integer number indicating the tree age in years (it is updated every 12 months)

Table 1: Entities and their attributes

Variable	Description
E_m	metabolic requirements of a mouse, namely a positive number indicating the energy consumed by a mouse every month
s_{max}	maximum number of seeds eatable in a month by a mouse
n_{oMAX}	maximum number of offspring per mouse per year
n_{mov}	maximum number of movements allowed in a month, namely maximum number of patches that a muse can explore in a month
pred	death probability for a mouse in month
p_d	death probability for a tree in a year
p_b	probability of a seed to germinate and hence to produce a new tree
A_r	age in which trees become reproductive, namely become able to produce seeds
mast	boolean variable indicating if seed production is uniform ($mast = FALSE$) or variable and synchronized ($mast = TRUE$)
S	average number of seeds produced in a year by a tree, in case of "no-mast"
n_y	number of years of a mast seeding period (it makes sense only when $mast = TRUE$)
prop	ratio between seeds in a "normal" year and in a mast seeding one (it makes sense only when $mast = TRUE$)

Table 2: Global variables and their description

3 Processes and scheduling

In each time step, mice eat (or, at least, look for food) and eventually die. Other routines occur only at some specific month, as summarized in Table 3.

time step number Month	0 Sep	1 Oct	2 Nov	3 Dec	4 Jan	5 Feb	6 Mar	7 Apr	8 May	9 Jun	10 Jul	11 Aug
Mice death	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Mice eating seeds		✓	✓	✓	✓	✓	✓					
Mice eating other	✓							✓	✓	✓	✓	✓
Mice reproduction		✓							✓			
Trees die							✓					
New trees grow up							✓					
Trees produce new seeds	✓											

Table 3: Time organization in the model. Time step numbers correspond to the result of the actual tick value modulus 12 operation.

4 Design concepts

4.1 Basic principles

- A basic principle underlying the model design is that mice require energy to live and derive their energy from food. In winter, seeds represent their major food source (Wolff et al. 1985). Therefore, mouse survival largely depends on seed availability, which is linked with the mouse/tree ratio. Reproduction also implies an energy cost. As a consequence, the number of offspring that each mouse can grow depends on its energy and, ultimately, on seed availability.
- We assumed an upper limit of food consumption for mice: even in presence of unlimited available resources, beyond a certain threshold mice become sated and stop eating (Ims 1990). In a given timespan, they can hence eat a limited amount of seeds given by the global parameter s_{max}. This is consistent with empirical observations on mice (and on any other animal as well). Note that the presence of an upper limit of food consumption represents the basic assumption underlying the predator satiation hypothesis.

4.2 Emergence

- We expect differences in the simulations outcomes depending on the state of the *mast* variable. Note that, even if *mast* in our model is implemented as a global variable, it directly affects only the behaviour of trees (more specifically, seed production). Following the predator satiation hypothesis, we expect that masting would favour the tree population, leading to a higher number of trees.
- To test the effect of masting, the model keeps constant the overall amount of seeds in both scenarios. In case of no-masting, the mean number of seeds produced by each tree S does not vary across years. In the masting scenario the mean number of seeds per tree varies from S_1 in "normal" years to S_2 in masting years. We set S_1 and S_2 in order to maintain the same average seed production per tree in both the *masting* and the *no-masting* conditions:

$$n_y \cdot S = (n_y - 1) \cdot S_1 + S_2 \tag{1}$$

  where n_y is the number of years of a mast cycle, i.e. the number of years between two consecutive mast events. This procedure guarantees that any difference between the model output in the *masting* and *no-masting* cases derives from changes in the distribution, and not in the overall amounts of seed production per tree.

4.3 Interaction

Trees affect mice through seed production, mice affect trees by eating seeds. Mice interaction is limited to resource consumption, i.e., by the fact that the seeds eaten by a mouse are no longer available for any other mouse. The more seeds mice eat, the more they survive and reproduce. Conversely, since eaten seeds do not germinate, fewer trees can grow up. If the tree number decline, even the seed production declines, causing a reduction of the mouse population.

4.4 Stochasticity

- Agents (trees and mice separately) perform their routines in a random order.
- The number of offspring generated by a mouse is a random number from 0 to the maximum one allowed by its current energy. In Summer months, when mice do not eat seeds, they eat a random quantity of energy from 0 to their upper limit s_{max}. Every month, a mouse has a probability *pred* of dying, even if it has enough energy to survive.

- The number of seed produced by a trees is a random number extracted from a normal distribution with mean S and standard deviation $S/4$ in the no-masting scenario and mean S_1 or S_2 and standard deviation $S_1/4$ and $S_2/4$ in the masting scenario (see Section 1).
- Each seed (not eaten by mice) has a germination probability p_b and each trees has a death probability p_d per year.

4.5 Observation

Fhe following data are collected from time step 1000 on (i.e., approximatively at the equilibrium):
- the maximum, the minimum and the average number of trees in the system;
- the maximum, the minimum and the average number of mice in the system;
- the maximum, the minimum and the average value of the colonization index *CI*.

The *CI* is computed as the ratio between the number of germinated seeds in a year and the number of empty patches in the simulated environment in the same year (in case of no empty patches, *CI* is forced to 1). We introduced this index to express the tree capacity of colonizing their environment and therefore their long term success. The mere number of trees is not able to capture this because mice affect only seeds and not standing trees. If no new trees grow up, their number declines due to p_d, but only after a certain delay. The *CI* indicator overcomes this drift-effect and directly measure the tree reproductive performance.

5 Initialization

- In all simulations, at the time step 0, trees are at their carrying capacity: i.e., 1600 trees on our 40×40 patch space. Their initial age is drawn from an uniform distribution in the $[0, 300]$ interval. The initial number of mice is set to 500. Their initial age and energy are set to zero.
- All other model parameters are based on empirical data. Some of them were varied within some ranges. The referring values and variability ranges are presented in Table 4.

6 Submodels

- *Mouse eating and death*

  Mice older than 36 months die because of their age. Younger mice die with a probability *pred* due to predation (or other events).

  Surviving mice increase their energy. In Summer months (Tab. 3) mice receive a random amount of energy in the $[0, s_{max}$ interval. In winter months each mouse performs the following steps:

  1. it moves towards the neighbouring patch containing the highest number of seeds (if its current patch is the one containing the highest number of seeds, it does not move)
  2. it eats all the available seeds, under the condition of not exceeding s_{max}
  3. if s_{max} is not reached, the previous steps are repeated for a maximum of n_{mov} times.

  As a consequence a mouse can preform at most n_{mov} movements across patches in a month: this is consistently with the fact that, in reality, mice move only within their own home range (Wood et al. 2010).

  Subsequently, the mouse energy balance is computed. If E is the energy eaten by a mouse in the current month, its energy E_t is given by:

  $$E_t = E_{t-1} + E - E_m \tag{2}$$

  where E_m is the monthly metabolic requirement. If $E_t \leq 0$, the mouse die (starvation). During winter, E is equal to the number of eaten seeds (the seed is used as energy unit).

	Parameter name	Description	Unit	Referring value	Variability range
Mice	E_m	metabolic requirements	number of seeds	8	
	s_{max}	maximum number of seeds eatable in a time step by a mouse	number of seeds	20	
	n_{oMAX}	maximum number of offspring per mouse per year	pure integer number	9	
	n_{mov}	maximum number of movements allowed in a time step	pure integer number	10	$8 \div 12$
	pred	death probability	pure number	0	$[0,1]$
	E_r	reproduction cost (calculated following equation 3)	number of seeds	16	
Trees	p_d	death probability in a year	pure number	0.035	$[0.03, 0.04]$
	p_b	probability of a seed to to produce a new tree	pure number	0.9	
	S	seeds produced in a year, in case of "no-mast"	pure integer number	650	$500 \div 800$
	A_r	age in which trees become reproductive	number of years	25	
Masting	n_y	number of years of a mast seeding period	pure integer number	5	$2 \div 8$
	prop	ratio between seeds in a "normal" year and in a mast seeding one	pure number	40	$10 \div 70$

Table 4: Overview of the model parameters.

- *Mouse reproduction*
  Each mouse generates a random number of offspring from 0 to the maximum allowed from its energy E_t. This theoretical maximum is given from E_t/E_r, where E_r is the energy reproduction cost for baby, which is computed following the relation:

$$n_{oMAX} = int\left[\frac{12(s_{max} - E_m)}{E_r}\right] \quad \Longrightarrow \quad E_r = \frac{12(s_{max} - E_m)}{n_{oMAX}} \tag{3}$$

  where n_{oMAX} is the maximum number of offspring that a mouse can generate in optimal conditions. This parameter, as other model parameters, has been set basing on empirical observations (the empirical number of offspring is actually divided by two, since our model does not distinguish between females and males).

- *Tree death*
  Trees have a death probability of p_d in the months 6 mod 12 (corresponding to March). Note that the model concentrates deaths in a single month, just before the germination of new seedlings. While this is clearly unrealistic, it bears no consequences for the dynamics of our system, where the fundamental issue is the number of trees that are alive during the reproduction period.

- *New trees grow up*
  In the germination month (March), new trees grow up in empty patches from uneaten seeds. Each seed has a probability p_b to germinate. Since each patch can support only a single tree, when a seed germinates in a given patch, all other seeds in the same location die. Seeds neither eaten nor germinated die, becoming no longer available neither for germination nor for eating.

- *Seeds spreading*

In the month 0 mod 12, corresponding to September, trees in reproductive age, i.e., with age $\geq A_r$, produce seeds and spread them in the neighbouring patches. The number of seeds produced by each tree is specified in Section 4.4.

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