

## Model Description for *hominin\_ecodynamics2.0.nlogo*

### OVERVIEW

**Purpose:** *hominin\_ecodynamics2.0* is designed as an experimental laboratory to explore the dynamics of biobehavioral interactions between two populations, and their genetic and demographic consequences. Specifically, the model is designed to study the effects of differing initial population sizes, different interaction distances, mating restrictions, and different fitness on the demography and spatial distributions of the original two populations and hybrids. Each agent has a genome with 10 loci and 2 possible alleles at each locus. Agents move and reproduce within “foraging radii” set by the user. Agents can reproduce by mating with another agent if one is present in the immediate vicinity or cloning themselves (simulating mating with a like agent) when another agent is not nearby. Offspring of mating between 2 agents inherit genomes from their parents by independent assortment. The user can set the birth rate and death rate for each original population and for hybrid offspring. The agents can be confined spatially to the geography of Pleistocene western Eurasia by means of a small graphic file map of this region, *w\_eurasia.png*. While the model is easily generalizable, as configured, it focuses on the interaction and biogeography of morphologically modern human and Neanderthals.

**State Variables and Scales:** Each **agent** (called a *variant*) represents an individual. Each individual has a *genome* that includes variable and non-variable loci. Initially, there are only 2 variants, those that are homozygous for the M allele at all variable loci and those that are homozygous for the N allele at all variable loci. All agents are homozygous for allele H in their non-variable loci. As agents interact and mate, agents with more diverse genomes are born (hatched in NetLogo terminology). Agents are assigned to a phenogenotype (*v-type*) on the basis of their gene frequencies to help track population dynamics: “MM” and “NN” for agents homozygous at all variable loci, “M-type” or “N-type” for agents with M or N allele frequencies respectively between 0.99

and 0.25, and “hybrid” for agents with M or N allele frequencies between 0.75 and 0.25. The model can be initialized with the 2 initial populations spatially segregated or agents of both initial populations can be randomly intermixed across the geographic space.

<i>Agent variables</i>	<i>Description</i>
<i>genome</i>	A 2 x n array in which each row is a gene locus
<i>Mcount</i>	Total number of M alleles in an agent's genome
<i>Ncount</i>	Total number of N alleles in an agent's genome
<i>Mfreq-indiv</i>	Frequency of M alleles among the variable loci in an agent's genome
<i>birthrate</i>	The probability that an agent will reproduce each cycle (1-1000/1000)
<i>deathrate</i>	The probability that an agent will die each cycle (1-1000/1000)
<i>v-type</i>	Variant type (phenotype) of agent (pop1, pop2, hybrid)
<i>home-x, home-y</i>	Coordinates of the agent's home-base patch. An agent can move within a radius (=fradius) around its home-base, but never shifts its home base.
<i>fradius</i>	Foraging radius. The distance from an agent's home-base patch that the agent can move (measured in patches)

**Patches** define the area within which agents move and interact. There are no variables assigned to patches beyond built-in NetLogo global variables. Agents are restricted to patches defined as “land”, which is identified by color. A png file that represents a map of Pleistocene western Eurasia can be used to define a geographically realistic land area in the simulation. Currently, land is automatically defined by the color of the patch at x=10, y=10 (patch coordinate values begin at the lower left [southwest] corner and increment to the upper right [north and east]). This could be changed to a user-selectable coordinate pair.

**Global variables** are used to initialize the agents and their world. Most can be set by the user.

<b><i>Global variables</i></b>	<b><i>Description</i></b>
<i>land-color</i>	The color of patch x=10, y=10
<i>land</i>	Agentset of all patches having a color (pcolor) of <i>land-color</i> . Agents can only move on patches defined as land
<i>land-patches</i>	The count of patches defined as land
<i>MM-number</i>	Initial number of agents with genotype MM.
<i>MNloci</i>	Number of variable loci in the agent genome
<i>Hloci</i>	Number of non-variable loci in the agent genome
<i>Mcolor</i>	Color of agents that are homozygous for M at all variable loci
<i>Ncolor</i>	Color of agents that are homozygous for N at all variable loci
<i>MM-birthrate</i>	Birthrate of agents with genotype MM.
<i>MM-deathrate</i>	Normal death rate of agents with genotype MM (see <i>crowding</i> ).
<i>MM-fradius</i>	Foraging (i.e. interaction) radius around home-base of each agent with genotype MM.
<i>NN-number</i>	Initial number of agents with genotype NN.
<i>NN-birthrate</i>	Birthrate of agents with genotype NN.
<i>NN-deathrate</i>	Normal death rate of agents with genotype NN (see <i>crowding</i> ).
<i>NN-fradius</i>	Foraging (i.e. interaction) radius around home-base of each agent with genotype HH NN
<i>hybrid-birthrate</i>	Birthrate of hybrid variants (with M allele or N allele frequencies between 0.25 and 0.75)
<i>hybrid-deathrate</i>	Normal death rate of agents with genotype Hh or hH (see <i>crowding</i> ).
<i>segregate</i>	When on, agents of populations 1 and 2 are initially distributed randomly on either side of a boundary set by the user (see <i>pop-boundary</i> ). When off, all agents are distributed randomly, simulating panmixia.
<i>pop-boundary</i>	When <i>segregate</i> is on, this represents the x-coordinate of the boundary between the initial distribution of populations 1 and 2.
<i>crowding</i>	When on, if the number of agents exceeds the number of land patches, the death rate is increased according to the formula:

	$[\text{new death rate}] = [\text{old death rate}] * ([\text{total agents}]/[\text{total land patches}])$
<i>avoidance</i>	Variable that determines strength of assortative mating.

**Process Overview and Scheduling:** Each cycle, each agent jumps from its home patch to a patch in a random direction and at a random distance that is less than or equal to the foraging radius. Each agent can reproduce if a randomly selected number between 1-1000 falls within the range of the agent's birthrate. Each time an agent reproduces (no more than once per cycle), it produces a single offspring. An agent will die if another randomly selected number between 1-1000 falls within the range of the agent's death rate. As described above, the death rate can be increased if *crowding* is on and the number of agents exceeds the number of land patches.

If an agent is able to reproduce, it looks for a potential mate (i.e., another agent) within a circle around its current position whose radius is the agent's foraging radius (*fradius*). If no potential mate is present, the agent clones itself; if one or more potential mates are present, one is chosen at random for mating. If *avoidance* = 0, then the 2 agents will mate and produce an offspring. If *avoidance* = 100 (100%), the chance that the 2 agents will mate is determined by their genetic similarity. Genetically identical individuals will always mate and individuals who are completely different genetically (e.g., MM and NN) will never mate. Otherwise, mating will be determined by strength of similarity. The strength of assortative mating is determined by the value of the *avoidance* variable.

If an agent mates with another agent, an independent assortment routine [Indep\_Assort] is run to give the offspring an equal chance of receiving alleles on chromosome 1 or 2 from each parent. If the offspring is a homozygote, M-type, or N-type, it takes on the birthrate and death rate of the relevant homozygous population (MM or NN); if it is a heterozygote it takes on the hybrid birth rate and death rate. Hybrids keep the foraging radius (*fradius*) of the reproducing agent rather than its mate.

The offspring then moves to a new patch on land that is randomly selected from patches in a circle whose radius is (*fradius*) + (a random distance within the range of *fradius*).

## DESIGN CONCEPTS

**Emergence** (a summary of emergent phenomena from the interaction of the agents). The primary emergent phenomenon is the variation in the numbers of each phenogenotype (MM, M-type, hybrid, N-type, NN), and M and N alleles over many cycles, in response to the initial numbers of agents, the foraging radius of each type of agent, agent fitness (birth and death rates), and assortative mating (*avoidance*). Assortative mating has surprisingly little impacts over long simulation runs. Changing foraging radius and relative initial population sizes can have large effects. Small foraging radii also seem to result in agent spatial clumping although there are no rules to either encourage or discourage clumping.

**Adaptation** (how the agents adapt their behavior to their and their environments current state): The environment does not vary; hence, agents do not adapt to the environment.

**Fitness/Objectives** (a summary of the agents' goals): The agents have no goals. They move, reproduce, and die. Their fitness is controlled by the user adjusting birthrate and death rate. Movement radius is also controlled by the user.

**Prediction** (how the agents predict the consequences of their decisions): The agents do not predict the consequences of their decisions.

**Sensing** (environmental variables perceived by the agents, which might include their own variables): Agents can sense when a move will take them off land; in that case they will attempt to jump to different patch. They also can sense another agent in their vicinity.

**Interactions:** Agents interact when one agent mates with another agent. The offspring inherits alleles from each of the two mating agents.

**Stochasticity:** Movement is stochastic around a home-base and within a foraging radius.

Reproduction and death are stochastic, with the chance of both (per 1000) determined by the user.

When 2 agents mate, the chance that either will pass to the offspring the alleles on chromosome 1 or 2 to the offspring is stochastic.

**Collectives** (whether the agents are grouped socially): The agents are not grouped socially, but are abstract representations of forager social groups.

**Observation** (how data are gathered from the model): The total numbers of agents of each phenogentotype (MM, M-type, hybrid, N-type, NN) are recorded, as are the total number of M and N alleles. Data may be gathered by the BehaviorSpace tool included in Netlogo, and may viewed on plots and monitors updated after each step of the simulation.

## DETAILS

**Initialization:** The model is initialized by pressing the “setup” button; most initial simulation values are specified by the user.

First, patches are initialized on the basis of a PNG file names “w\_eurasia.png “. A file by this name must exist in the same directory as the simulation file in order for patches to be initialized in the geographical configuration of western Eurasia. Otherwise, the world the agents inhabit will be a simple rectangle. Currently, the world size (x and y dimensions) is set to the x and y dimensions (in pixels) of “w\_eurasia.png”. The agentset *land* is then defined as all patches with the same color as pixel x=10, y=10 in “w\_eurasia.png”.

Next, 2 populations of agents are initialized; the initial numbers of agents in each population is set by the user. All agents in population 1 have a genotype of MM, a birthrate of *MM-birthrate*, a deathrate of *MM-deathrate*, and a movement radius of *MM-fradius*; all agents in population 2 have a genotype of NN, a birthrate of *NN-birthrate*, a deathrate of *NN-deathrate*, and a movement radius of

NN-*fradius*. If *segregation* is off, all agents are distributed randomly across patches defined as land.

If *segregation* is on, agents of population 1 are randomly distributed to the left of an x-coordinate set by the user (*pop-boundary*) and agents of population 2 are randomly distributed to the right of the *pop-boundary* x-coordinate.

**Input:** No Input data are necessary for the model.

### **Submodels:**

**Check\_Death:** An agent dies (is removed from the simulation) if a random number between 1-1000 (generated each cycle for each agent) falls within the range set as the death rate for the agent's phenotype.

**Reproduce:** If a random number between 1-1000 (generated each cycle for each agent) falls within the range set as the birthrate for the agent's phenotype, the agent "hatches" an offspring. If there is no other agent on a patch within a circle whose radius is *fradius*, the agent hatches an offspring by cloning itself. If 1 or more agents are found on a patch within this circle, 1 of these agents are chosen at random as a mate and submodel *Indep\_Assort* is run.

**Indep\_Assort [mate]:** This determines which of an offspring's parents' alleles it will inherit. Random numbers (0-1) determine which of the offspring's chromosomes is inherited from each parent, and which 1 of the parents' alleles are inherited on each of the offspring's chromosomes.

### **Access to Agent-Based Model Code**

The agent-based simulation of MMH/Neanderthal biobehavioral interaction is written in NetLogo version 4.1.3. NetLogo can be obtained, free of charge from Northwestern University, at <http://ccl.northwestern.edu/netlogo/>. Both the model and a copy of the detailed model description above can be obtained through the CoMSES Computational Model Library at

<http://www.openabm.org>. The model file, *hominin\_ecodynamics2.0.nlogo*, includes code and summary documentation of its use and operation.

The model is normally run from within NetLogo. Alternatively, an html version of the model (*hominin\_ecodynamics1.0.html*) can be run from a browser if the appropriate *NetLogoLite.jar* file is in the same directory as the model (included with the model package) and a current version of Java is installed on the user's computer. The file *w\_eurasia.png* (a background map) must also be in the same directory as the model if a western Eurasia background map is desired. Without the background map, the model runs in a simple, rectangular world. Opening the model within NetLogo also permits the model code to be examined.

For either method of access, the user should set desired parameters using the GUI tools (sliders and switches), press the “setup” button to instantiate all agents, and press the “run” button to start the model. In addition to the description above, instructions for running the model can be found in the model files themselves.