

Model description

This supplement section is a description of our model (`lgm_ecodynamics1.0.nlogo`) following the Overview Design and Details (ODD) Protocol described by Grimm et al. [1,2]. This version of the model is used in [our paper citation].

The model is adapted from a model by Barton and Riel-Salvatore [3] of modern human and Neanderthal interaction in Western Europe.

Overview

Purpose

`lgm_ecodynamics1.0` is a modification of `hominin_ecodynamics2.0` designed by Barton and Riel-Salvatore [3]. The model uses the NetLogo toolkit for coding [4]. The purpose of the current version is to experiment with the effect of behaviours governing cultural interactions and mobility between the Last Glacial Maximum (LGM) populations of Western Europe. The principle hypothesis we are evaluating what was the impact of different scales of mobility on the size and level of connectivity between sub-populations, as well as their genetic makeup? And was this effect sufficient to maintain distinct material culture groupings that are reflected in the archaeological record?

We model individual hunter-gatherer household mobility within a foraging territory and their interaction with other households in the vicinity. The model is designed to study the degree of inter-regional interaction between households under different behavioural conditions, such as population size, foraging radius, and reproductive rates, and different environmental conditions, such as heterogeneity in suitable habitat.

There are three primary differences between Barton and Riel-Salvatore's model and our `lgm_ecodynamics1.0`. Firstly, we are modelling only modern humans instead of modern humans and Neanderthals so all of our agents have the same behavioural characteristics. Secondly, we use a set of six geographic markers to track inter-regional mobility rather than modern human and Neanderthal genetic alleles. Finally, rather than model a homogenous landscape, we import a heterogeneous landscape based on a predictive model of habitat suitability from Burke et al. [5]. This creates discontinuities in mobility patterns in response to the availability of suitable habitat.

Entities, state variables, and scales

Each **agent** represents a "household", i.e., a small family group of hunter-gatherers. Agents have an X,Y coordinate representing the center of their foraging territory (*home_patch*). We assign a *trait_list* to each agent that is a 2 x 100 array representing their genome. Each row of the array is

a gene locus with two positions and one of six geographic alleles at each position. The agents then have a number of counter variables to track the frequency of each geographic allele within their genome. Lastly, agents have an age variable that tracks how many time-steps of the model since they formed.

The model landscape is a raster grid of 5 x 5 km cells called **patches**. Patches are assigned a *suitability* value ranging from 0 to 1 using an imported raster map, and are based on a predictive model published elsewhere [5]. Suitability is imported as a raster map with 1 km resolution but is re-sampled on import to ~5 km resolution. Cells representing ocean or a glacier are given a null value (“NaN” or not a number in NetLogo terminology). Patches are assigned to a *core* numbered from 1 to 6 based on the number of clusters of high habitat suitability (HS) cells identified during spatial analysis (see main text for GIS methodology). The majority of cells are not within one of these high HS cells and are assigned a null *core* value. We assign a broader *region* variable that follows the same numbering as *region* but is not restricted to high HG clusters with a third imported raster map. We track the cumulative land use of agents using an occupation frequency counter on each patch, *occfreq*. The *occfreq* map may be exported at the end of a run to see where on the landscape the population of agents spent the most time. Cells have a *fallow* flag that is marked *true* for one timestep following an occupation. Fallow cells are considered ineligible for movement, but are reset to *false* before the next day’s movement.

Several **global** variables are assigned either by the user in the GUI or within the model setup. These make up the behavioural parameters related to demography and mobility of the agents.

Global vars.	Description
fradius	Foraging radius. The distance in patches an agent may move from its home_patch.
birthrate	The probability that an agent will reproduce each timestep if in range of another agent.
trait_list_size	An optional parameter to change the length of the genome (set to 100 in the current paper).
number	Initial population size in number of agents.
idw-weight	Parameter controlling the probability of movement at high distances from the home_patch. Higher weighting results in agents being more likely to select a closer patch. (default = 2.0)
weight-move?	Switch off for random mobility, on for HS to be factored into the probability of selecting a cell.
hs_death?	Switch on for HS to be factored into the probability of death.
hs_benefit	Percent increased survival odds on cells with suitability = 1.0 compared to the baseline at cells with suitability = 0.5. Range 0 to 1 at 0.25 increments.

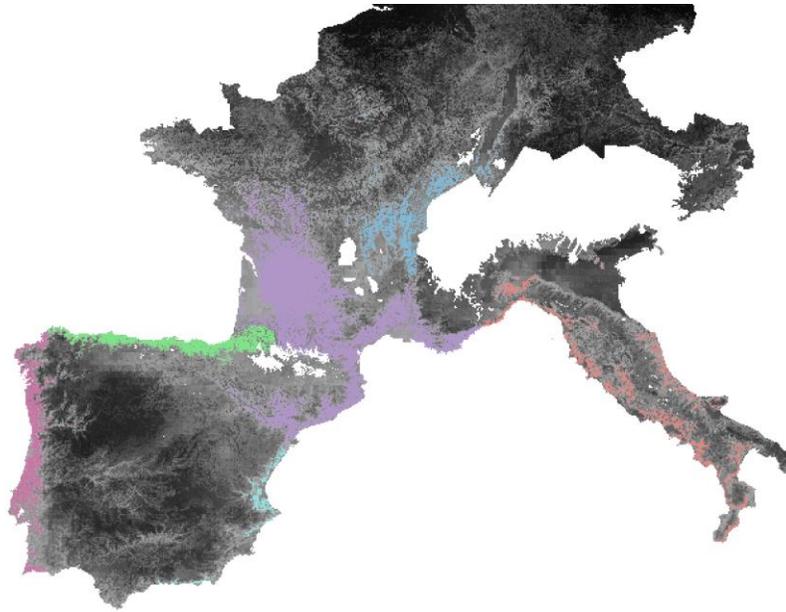


Fig. S1: The model's landscape. Grey scale values show suitability from 0=black to 1=white. Patches with a “core” value are shown with a colour instead of in greyscale.

Process overview and scheduling

In each time step, which represents one month, each agent moves from its *home_patch* to a cell within its foraging radius. The probability that any given cell is chosen may be weighted by its habitat suitability value, if *weight-move?* is on, and its distance from the *home_patch*, if *idw-weight* is greater than zero (also known as a roulette wheel selection [6]). To save computational processing time, since at large radii runs can take longer than a week, we use a random sub-sample of 200 cells in the weighted random selection. If any agent finds fewer than 200 cells in its radius (e.g. because many are ocean) the model switches to evaluating all cells in the radius. If *weight-move?* is off, then weighted random cell based only on distance within the foraging radius is chosen. See submodels section below for additional details on IDW and the weighted random selection of cells.

The agent then has a probability of fissioning to create an offspring agent at a probability equal to the birthrate. If a reproduction event is to occur, the agent looks for the nearest agent to be the “mate” and an independent assortment routine (*Indep_Assort*) routine is run to produce a combination of their *trait_lists* (see Submodels).

Lastly, we run a death routine which gives each agent (excepting those created during the same timestep) a probability of disbanding. The base *deathrate* is equal to the *birthrate*, but if *hs_death?* is on, that *deathrate* is adjusted based on the habitat suitability value of their cell such that lower HS decreases their probability of survival (see *hs_death* submodule below).

When the run is finished (model default is 3000 time steps representing 250 years), the model exports a wide variety of data. The most important two for the present paper are: 1) the population size, or count of agents, of each *region_count* area, 2) the frequency of each genetic trait within each *region_count* area, and 3) a map of the occupation frequency of each cell (*occfreq*).

Design Concepts

Basic principles

A basic principle of this version of the model is that agents, called “groups” in the model code, maintain home range fidelity. That is, while groups are mobile within a foraging radius of their home cell, they do not venture beyond that radius. Offspring groups establish their own home within *fradius* of the location of their parent group at the time of their reproduction (which may be beyond the *fradius* of the parent group’s *home_patch*).

Another basic principle is that groups are aware of and are able to predict the *suitability* of the landscape for foraging and that they use that information in mobility decisions. We referred to this capacity as spatial foresight in a previous publication [7,8]. The weighted random walk procedure estimates this behaviour without the fixed percent error used in our previous article. Agents also cannot occupy an already occupied cell or one that an agent occupied in the previous timestep, i.e. marked “fallow”.

Emergence

The variation in the populations of each region, and the amount of genetic influence from other regions, emerges from a combination of the group’s behavioural profile (foraging radius, birthrates, deathrates adjusted or not by habitat *suitability*), the chance pattern of interaction in a given run (i.e. path dependency), and the heterogeneous spatial distribution of habitat suitability (when *weight-move?* and/or *hs_death?* are on).

Adaptation

The environment does not change (ie. agents do not consume the habitat during foraging) and the groups do not change their behavioural profile in response to their environment. The “genetic” markers are neutral with respect to the environment, so there are no evolutionary processes over generations that affect their behaviour.

Objectives

The groups have the goal of selecting higher suitability habitat cells but they are not perfect maximisers. Rather their decision is only weighted towards cells with higher *suitability*. That is, on any given time step they **may** move from a higher suitability to lower by chance.

Learning

The groups do not learn. While they may acquire new regional traits, these traits are neutral with respect to their behaviours.

Prediction

The groups do not predict the future state of the environment (which does not change) or any aspect of other groups' behaviour. They only read the current state of the landscape and the positions of other agents.

Sensing

The groups sense ocean and glacier cells to avoid them. They sense other groups within their foraging radius as a part of the reproduction procedure and during movement (i.e. to avoid moving to an already occupied cell). They sense the habitat suitability values and distances of patches as a part of their mobility.

Interaction

Groups affect each other's mobility since groups may only move to empty cells. Groups interact during the *reproduction* procedure where they combine their *trait_lists* to make the offspring group's *trait_list* (see submodels below).

Stochasticity

Several elements of the model are stochastic. By NetLogo's default, the model randomises the order in which groups take their turn within a time step. Groups' initial locations are chosen randomly from patches with a *region* number (i.e. not ocean or glaciers). For each group, movement is to a weighted randomly selected cell within the foraging radius of their *home_patch*. Probabilities of fissioning and disbanding also rely on comparing a randomly generated number to the *birthrate* and *deathrate* for each agent each time step to determine whether or not a fission or a disbanding will take place. Finally, the *Indep_Assort* procedure randomizes from which parent each allele is copied into new agent's genomes.

Collectives

Ad hoc collectives of groups determined by the agents' *region* are used for sub-setting the data analysis at the end of runs. Agents have no awareness of other agents' genomes, e.g. for use in extra attraction or avoidance behaviours.

Observation

We count the final population size of each *region*. We measure the mean allele frequencies of each region. Finally, we export a raster map showing the summed occupation frequency of each patch over the whole run (*occfreq*).

Details

Initialization

The model initializes when the user presses the setup button on the GUI. Firstly, the model imports the three raster maps, *suitability*, *core*, and *region* to create the patch landscape. It then creates a sub-set of *land* patches and scales their colour value using the *suitability* patch variable.

Next, the model creates the initial population of agents and randomly distributed across patches with a *region* number. The agents set their *home_patch* to their current patch.

During initialization, if *hs_death?* is on, the setup also solves for *death_slope* and *death_yintercept* of a simple linear equation that will determine the variable *deathrate* on cells of different habitat *suitability*. The model assumes deathrate at suitability = 0.5 will be equal to birthrate then sets deathrate at suitability = 1.0 to be *hs_benefit* % lower. That is:

$$deathrate_{hs_{1.0}} = deathrate_{hs_{0.5}} - (birthrate * hs_benefit)$$

The slope and y-intercept of the linear equation is solved with basic algebra:

$$death_slope = \frac{(deathrate_{hs_{1.0}} - deathrate_{hs_{0.5}})}{1 - 0.5}$$

$$death_yintercept = deathrate_{hs_{1.0}} + (-1 * death_slope)$$

Input data

No additional input data are needed other than the three raster maps.

Submodels

Reproduce: If a random floating point number between 0 and 1 falls below the *birthrate* value, the group creates an offspring and searches for the nearest other agent within its *fradius* to be its mate. If no mate is found, the offspring is simply a clone of the parent. If a mate is found then *Indep_Assort* is run to produce a combination of their genomes in the offspring.

The offspring group then moves to a random unoccupied and *fallow = false* cell within *fradius* distance of the parent group's current cell, and then sets this new patch as its *home_patch*. The new group also sets its *age* to 0 so that it may skip the death routine for that time step.

Indep_Assort [mate]: This submodel is run by groups within *Reproduce* submodel and takes a target group as a parameter. For each position in the group's 2 x 100 array *trait_list*, an allele from a random one of the parents (the original group or the one selected to be mate) is copied into that position in the *trait_list*. The result is a randomized combination of traits that is, only on average, a 50% representation of the traits of each parent group.

hs_check_death: This submodel uses the *deathrate* parameter value to determine the likelihood of a group disbanding on a given time step. However, unlike *Reproduce*, when *hs_death?* is on it also adjusts that likelihood in response to the HS value of the group's current cell. As noted above, the base deathrate value is set equal to the birthrate during the setup procedure. In this submodel, a random floating point value between 0 and 1 is less than the result of the following formula to determine if the group disbands:

$$(death_slope * suitability) + death_yintercept$$

This equation linearly adjusts the *deathrate* of each group, on a per timestep basis, such that groups with higher *suitability* cells are less likely to disband. The *hs_benefit* parameter controls the magnitude of the benefit via the calculation of *death_slope* and *death_yintercept* in the model initialization (see Fig. 3).

randidw [fradius]: Random walk weighted with inverse distance weighting uses the *idw-weight* parameter to control the degree to which closer cells are favoured using the equation:

$$(d + 1)^{-w}$$

where *d* is distance of the cell and *w* is the *idw-weight* parameter. Since the circumference of a circle increases with distance, there are more cells at each sequential distance band. With an *idw-weight* of 0, groups are more likely to have moved farther away. This is an unintuitive result of using a random walk based on random selection of cells in a specified radius. For an *idw-weight* of 1, groups are more or less equally likely to choose a cell at any distance. For an *idw-weight* of 2, groups are more likely to choose a cell that is closer (Fig. S2). We select *idw-weight = 2.0* as our default value since shorter moves are less energetically costly and should be favoured by

groups. Once the weightings are determined, the model selects one cell using the Rnd extension by Payette [6].

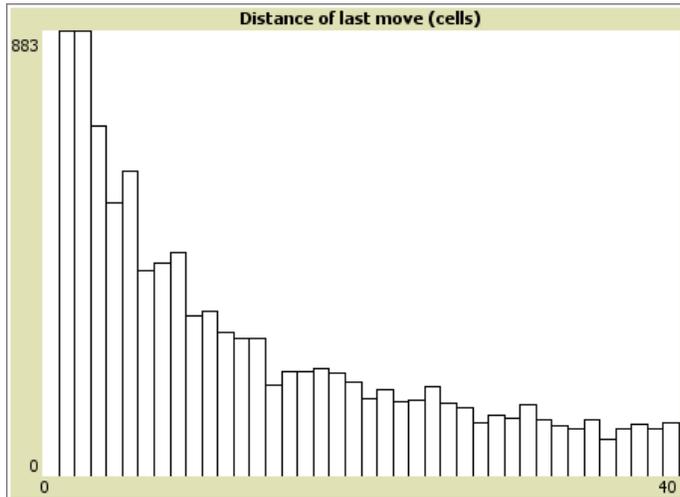


Fig. S2: Histogram of all agents' last movement distance when *idw-weight* = 2.0.

wrsidw [*fradius*]: Random walk weighted by the *suitability* cell value (*hs*) of a group's current location and inverse distance weighting:

$$hs * (d + 1)^{-w}$$

wrsidw_n200 [*fradius*]: Same equation as *wrsidw* but the model randomly selects 200 cells within the *fradius* for evaluation.

wrs and *wrs_n200* [*fradius*]: If *idw-weight* = 0, the model only uses the *suitability* value in the weighted random walk. n.b. In this paper, *idw-weight* is held constant at 2 so these submodels are unused.

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