Neanderthal replacement

Christina Isaicu 260578661
McGill University

Introduction

Neanderthals, a hominin species that had inhabited Europe and Asia for nearly 400K years, reached extinction around 35K to 40K years ago following the arrival of modern humans in those areas. Was their replacement by Moderns due merely to drift caused by population size differences or unidirectional migration? Or were Modern humans more fit for survival than Neanderthals? The model for simulating this replacement proposed by Daniel Shultz et al.[3] bridges the shortcomings found in models that exclusively consider fitness or drift explanations. Results suggest that although Modern fixation can occur through neutral drift given specific initial parameters, differential fitness between Neanderthals and Moderns provides a more general, reliable explanation for Neanderthal replacement. My model expands on this to include lateral movement that reflects a spatial schema. The results show that initial trends are supported by this new model, but the new model introduces a layer of complexity that requires more rigorous means of interpretation.

Method

I have extended the Stochastic Bi-directional Stepping-stone (SBS) model implemented by Shultz et al. from a linear configuration to two dimensions. This extension creates an array called a cellular automaton which is used to simulate population dynamics, particularly among predator/prey relationships.[1] Whereas the one-dimensional (1D) model has one point of contact between Neanderthal and Modern populations, the two-dimensional (2D) model

introduces a conflict border (or borders) of variable length that reflect spatial geography. The original left/right configuration of Neanderthals and Moderns representing the orientation of Europe and Africa is reflected in the 2D model through an initial North/South placement of the two populations. Like the original model, each cell, or band, represents hominin bands of unspecified size. Similarly, the updated model is stochastic and multi-directional, meaning that each time cycle, one band is chosen for death at random, and the movement of either population can happen in any direction. A schematic representation for the model is presented in figure 1.
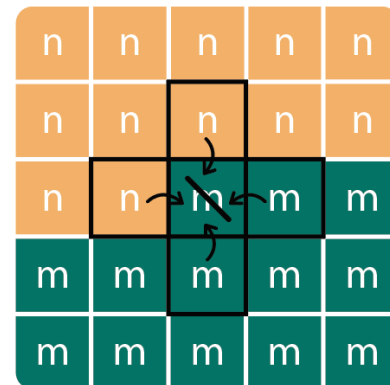
Figure 1: Neanderthal bands are labeled n, Modern bands m. The European continent tis indicated with a yellow background, Africa with green background. The dying band is crossed out with a black line, and the arrows indicate the direction of replication by its neighbors. Neighboring bands are outlined in black.

In the original model, individual bands had at most a neighbor to the left and right. The new model implements a von Neumann neighbourhood, where a band can have neighbors to the left, right, above, and below. When a band dies, it is replaced by the same type expressed in one of the adjacent bands. The probability of a band being

chosen for replication is determined by the neighboring types and their fitness. In the 1D model, the fitness of each type is fixed because a dying band at the conflict border is always flanked by exactly one band of each type. The new model introduces a variable bias in which the initial fitness is adjusted according to the types of neighbors bordering the dying band, and an additional costal advantage included within the initial parameters. The formula to calculate this bias is as follows:

$$Bias = Fitness + 0.02*(T \pm L \pm R \pm B)$$

T represents the bias value for the top neighbor, L represents left, R is right, and B is the bias value for the bottom neighbor. A modern neighbor (m) is assigned a value of +1, a Neanderthal neighbor (n) is assigned a value of -1, and the initial parameter for costal advantage (which will be further explained below) can be either +1, -1, or 0 for each type. The variable value of 2% is based on the initial SBS model which suggests that even a 1% increase or decrease in bias from neutral drift has a significant impact on fixation outcome. As we will see later on, the variable bias will only ever be at most $\pm$ ¾ of 2%, which is a 1.5% advantage or disadvantage. The bias is calculated this way because the proportion of "allies" bordering a dying band have an effect on the likelihood of its replacement, regardless the fitness of that type. The three death-birth scenarios are described below.

Scenarios
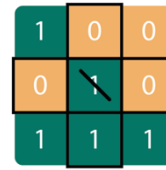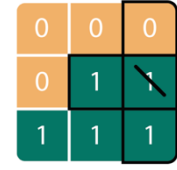

Figure 2.   *Figure 3.*   *Figure 4.*

Scenario 1:
All neighbors of the dying band are of the same type. The dying band has a 1.0 chance of being replaced by the type expressed in its neighbors. If the dying band is of the same type as its neighbors, the conflict border is not changed. For example, in Figure 2 the dying band will be replaced by a Modern band.

Scenario 2:
The four neighbors of the dying band are a mixture of both types. The weighted advantage is calculated using the formula given above. For example, in Figure 3 the dying band is bordered by three Neanderthal and one Modern band. If the initial fitness is 0.52 in favour of Moderns, then the weighted bias will be $0.52 + 0.02*(-1-1-1+1) = 0.52 + 0.02*(-2/4) = 0.51$. Although the fitness of Moderns is weighed in their favour, the higher proportion of Neanderthal neighbors shifts the bias slightly.

Scenario 3:
The dying band borders a coast. In Figure 4, the dying band has no neighbor to its right. The initial costal advantage parameter indicates whether each type has an advantage (+1), disadvantage (-1), or neither (0) at the coast. For example, if the initial parameter settings are as follows: Modern fitness = 0.52, costal advantage for Neanderthals (advx) = 0, costal advantage for Moderns (advy) = 1, the weighted bias would be $0.52 + 0.02 * (-1 + 1 + 1 + 1) = 0.53$.

Results

Simulation results are organized in the following order: differential fitness, relative population size, neutral drift, border tracking, and band lifespan. Simulations were run until fixation was reached and replicated 20 times per setting and plotted against results from the SBS model. Box plots are used to display the range and median of the data, which more effectively represents the data at such a small number of replications, compared to plotting the means.

Effects of differential fitness.

Both models were run at variable bias between $0.1 - 0.9$ in favor of Moderns, at a population ratio of 33:67 Neanderthal:Moderns (N:M). Studies suggest that the population of Modern humans was much higher than that of Neanderthals.[2] For reasons that will be discussed in the discussion section, the population ratio of 1:2 N:M was chosen for this study. The bias of 0.5 (neutral drift) was omitted from the following graphs because the high number of cycles obscured the rest of the values given the scale. The isolated graph of the 2D model is also included for further clarity. The 2D model had much fewer cycles and a much smaller range of data, however the trend seems similar to that of the 1D model.
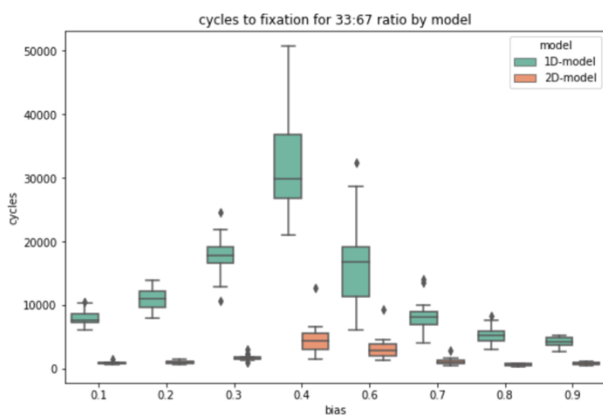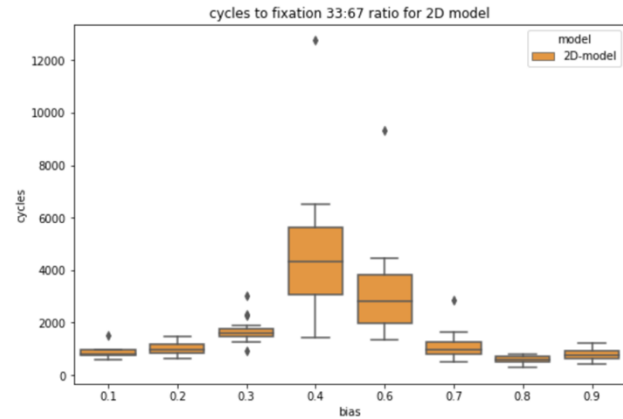

Figure 5.

Figure 6.

Effects of relative population.

Modern fitness calculated from recent studies suggest Modern humans had a fitness advantage of 0.61 or 0.71 considering Neanderthal additive or recessive mutations. 0.67 was chosen as a rounded average between the two values. As seen above, the 2D model reflects the trend resulting from the 1D model, but fixation is completed in much fewer cycles (about a tenth of those achieved by 1D model), and data is much less distributed.
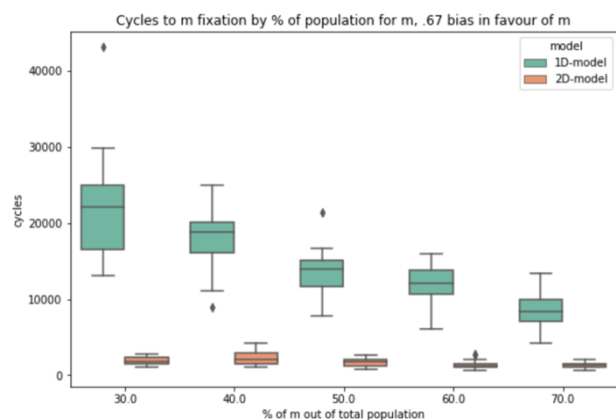

Figure 7.

Figure 8.

Neutral drift.

A population ratio of 50:50 and 33:67 at .5 bias ran up 500,000 + cycles each without fixation. For reasons to be discussed in the discussion section, no further analysis could be done beyond that.

Border incursions.

Border tracking is a feature that was removed because the implementation would have been vastly different for the 2D model, and time limitations prevented further inquiry towards a solution. However, I did include a function (printpopulation) to print a visual progression of simulations to fixation. The total hominin population is not actually stored in a 2D array but a vector structure. The 2D orientation is a visual aid to help interpret the results.
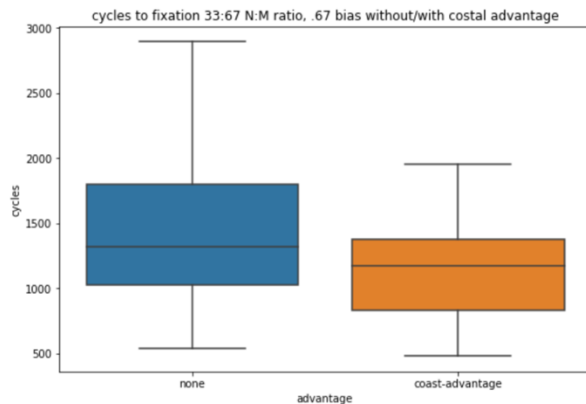

Figure 9.

Two animations accompany this report. **1-33-0-0-67-1-0-067.mov** is a simulation with the following parameters: 1 replication of: total hominin population is 100, made up of 33 0's and 67 1's. Neither population has an advantage at the border, and the bias is 0.67 in favor of 1's (i.e. Moderns).

1-33-0--1-67-1-1-067.mov follows similar parameters, except 0 is at a disadvantage at the border, and 1 has an advantage. Notice how 1s favour the coast in the second simulation, occupying the top row much sooner than in the unbiased simulation. It's also interesting to note that simulations in which a costal (dis)advantage is applied more cycles to reach fixation than those without, as shown in Figure 9. In both cases, Neanderthal (represented by 0) incursions into Modern territory is not substantial, but small numbers of bands do make it a few layers in. Of course, it's important to remember that although interesting, these animations represent but two replications, and border data would need to be implemented for further analysis.

Discussion

The number of cycles to fixation in the new model are far fewer than the SBS model, by up to a factor of 10 for equivalent parameter settings. What does this say about the plausibility of these results translated to lifespans in empirical time? Empirical data suggests that 10K years of contact between Neanderthals and Moderns is required for replacement.[3] The following calculation is drawn from the framework provided by Shultz et al. to calculate band lifespans.[3] Using the new model, 20 replications of 33:67 N:M ratio at 0.67 bias has a mean of 1173.35 cycles and a median of 1170.5 cycles. Using the mean, we divide 1173 cycles to fixation by 10,000 cycles to replacement to estimate the number of cycles

per year (= 0.1173) (or one cycle happens about every 8.5 years). If a band lifespan in cycles is 100, band lifespan in years is 100/0.1173 = 852.5. Using the same parameters and calculations for the SBS model, the mean cycles to fixation is 9140.65, so the average band lifespan is about 109.40, which seems to be an acceptable value according to the Shultz et al. systematic examination of band lifespans at varying degrees of fitness and population proportion.[3] What do these values mean? A band lifespan of 852 years means a band will exist for about 852 years before dying out, which allows plenty of time to reproduce. This value may not be empirically reliable, however, because it is unclear what the conditions of contact are for replacement to occur within 10K years. A band on the border between Neanderthals and Moderns has one of each type of neighbor in the SBS model, but that ratio varies in the new model.

Would Neanderthal replacement take less time if surrounded by Moderns on three fronts instead of one? This would require a more variable function to be implemented than the one available. Furthermore, although the chance of death for each band is still 0.01, the chance for death occurring at a border increases from 0.02 in the original model (2 bands at a border) to anywhere from 0.03-0.2+, as border length can vary. This can explain why fewer cycles are required to fixation, because there is a higher chance that a dying band is at a border. These fewer cycles also contribute to the larger band lifespans. Revisiting the 5000K+ cycles required for fixation at 33:67 initial population with a 0.5 bias, the band lifespan would be about 2 years which is not long enough for a hominin to reach maturity. This could be used to argue that this model favours against neutral drift.

Things to improve:

Implementation details:
- Introduce a new parameter *length* such that the population will always be a square of the length. At the moment the user needs to ensure nx+ny is a square number (such as 33+67), but if nx and ny represented proportion of population instead of totals, this would cut out user errors.
- The von Neumann neighborhood model ignores diagonal neighbors in favour of those directly beside or above a death band. The issue with a Moore model, which doesn't ignore the diagonals, is that the distances to the death band would not be equal. Consider a hexagonal cellular model so all neighbors are of equal distance to the selected band.
- Refactor printpopulation function to print output to a file and automate process that generates the animation.
- Refactor code for efficiency. The algorithms implemented in the 2D model are very slow, so simulations involving neutral drift could not be run to fixation.

Model:
- If n represents the total population of hominins, each band has a 1/n chance of dying per cycle. That may work well in 1D structure, but not likely in 2D. Create a function to randomly select multiple band deaths per cycle.

Is this model useful?
The spatial complexity of population dynamics requires more rigorous analysis than is available given the scope of this project. The new model confirms that differential fitness is a favourable explanation for Neanderthal replacement but barring any additional insights and limitations of systematic analysis, it may simply be introducing unnecessary specificity and complexity.

References

1. Jafelice, R. M., & Silva, P. N. Studies on Population Dynamics Using Cellular Automata. Cellular Automata - Simplicity Behind Complexity. (2011). doi:10.5772/15939
2. Kolodny, O. & Feldman, M. W. A parsimonious neutral model suggests Neanderthal replacement was determined by migration and random species drift. Nat. Commun. 8, 1–12 (2017).
3. Shultz, D. R. & Montrey, M. & Shultz, T. R. Comparing fitness and drift explanations of Neanderthal replacement. ArXiv:1810.12397 [q-Bio]