Supplementary Information
Comparing fitness and drift explanations of Neanderthal replacement

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This file contains supplementary information on:

1. Defining fitness and drift
2. Individual simulation runs illustrating border tracking and incursion
3. Speciation, competitive exclusion, interbreeding, and genetic assimilation
4. Array based models
5. Analytical predictions using random walks

1. Defining fitness and drift

Biological fitness is determined by the frequency at which the unit of study (alleles, traits, organisms, and average frequencies in populations and species) replicates itself in subsequent generations [1]. A unit producing more copies has higher fitness than a similar unit in the same environment producing less. Fitness is thus relative, changing with the environment and the existence of other units. For this reason, climate change models, sometimes proposed as a factor in Neanderthal extinction [2–4], should properly be classified as fitness models. Environmental shifts affecting the viability of Neanderthals, but not Moderns, ultimately indicate a Modern fitness advantage in the new environment. Upon identifying a unit replicating with increasing frequency relative to competitors, there are two possible explanations: 1) the unit has higher fitness, or 2) replication frequency is increasing due to drift, via random sampling. In the former, higher fitness means the unit undergoes natural and/or sexual selection more successfully than competitors. In the latter, fitness difference is absent, and the process is entirely stochastic. In life, neutral evolution (drift) is always operative as part of the landscape in which natural selection occurs. Rigorous theoretical modeling experiments have demonstrated that under both fitness and drift (due to random sampling), when units are competing for finite replication locations, there is eventual fixation on one type [5,6]. This is relevant for closely related species like Neanderthals and Moderns, exploiting similar niches in an environment with a finite carrying capacity. Therein lies a problem of equifinality, as both fitness and drift can lead to an identical end result, fixation (i.e. replacement).

One solution to distinguish whether fitness or drift is responsible for a replacement event

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is to determine what fitness advantage the replacing unit may have had. If one can be identified, fitness is the main driver – if not, the process is neutral. This is largely the path the Neanderthal replacement debate has taken. One problem with this approach is that fitness has modern cultural connotations of mental and/or physical superiority. However, biological fitness can be much more subtle, referring not to intelligence or physical prowess per se, but only to an increased probability of replication, whatever the cause. Small fitness advantages may be invisible archaeologically, particularly in similar complex organisms like Neanderthals and Moderns. A small net fitness difference in these cases could be the combined effect of hundreds of minute genetic features, difficult to identify with limited knowledge and data. This makes it all the more difficult to ascribe a replacement event to fitness. Likewise, ascribing a replacement event to neutral drift requires justifying any preconditions (such as a larger starting population and asymmetrical migration rate and direction) as the result of exogenous environmental factors rather than fitness difference. This is also difficult to prove empirically. Unequivocally attributing a replacement event to either a particular fitness difference or neutral drift can therefore be difficult.

2. Individual simulation runs illustrating border tracking and incursion

This section provides some additional background on measuring border tracking and incursion across the initial border in our simulations. Figure S2 presents an example plot of a single run, which starts with 33 Neanderthal bands and 67 Modern bands, and a Modern fitness advantage of .67. In these simulations, one band is randomly select to die at each time cycle. There is considerable variation in these border plots; what they have in common is that they are not monotonic.

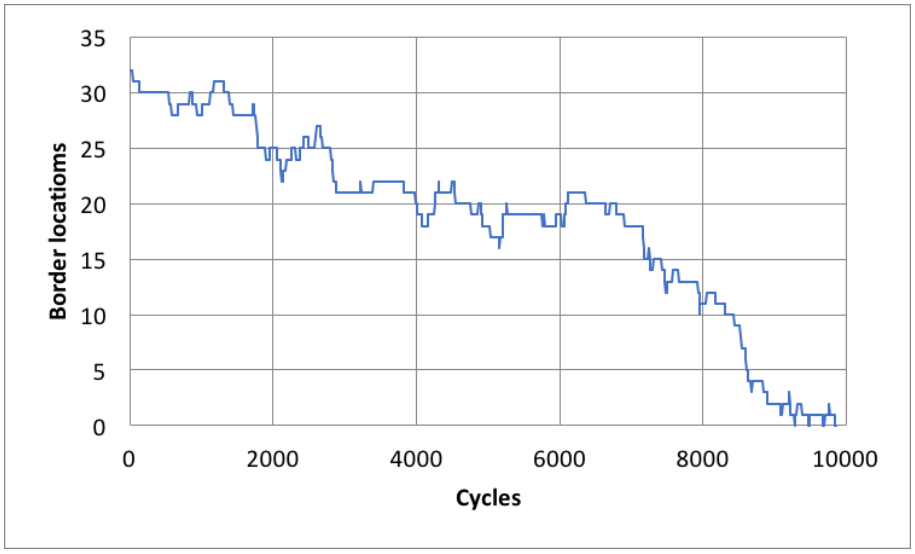

Figure S1. Example of border tracking in one replication with initial populations at 33 Neanderthal bands and 67 Modern bands, and Modern fitness of .67.

As noted in the main paper, such border tracking enables identification of incursions across the initial border between Neanderthals and Moderns. Our incursion index computes the sum of Neanderthal incursion distances across the initial border, at each

time cycle. This integrates time frequencies and spatial distance spent across the border. Two examples of replicate incursions are presented in Figures S2 and S3, with the initial border represented by a horizontal red line. Both example simulations start with 25 Neanderthal bands and 75 Modern bands. The plot in Figure S2 is based on neutral drift, with a Modern fitness of .5; that in Figure S3 uses a Modern fitness of .6. Notice that there are considerably more and deeper Neanderthal incursions under neutral drift than with Modern fitness of .6.

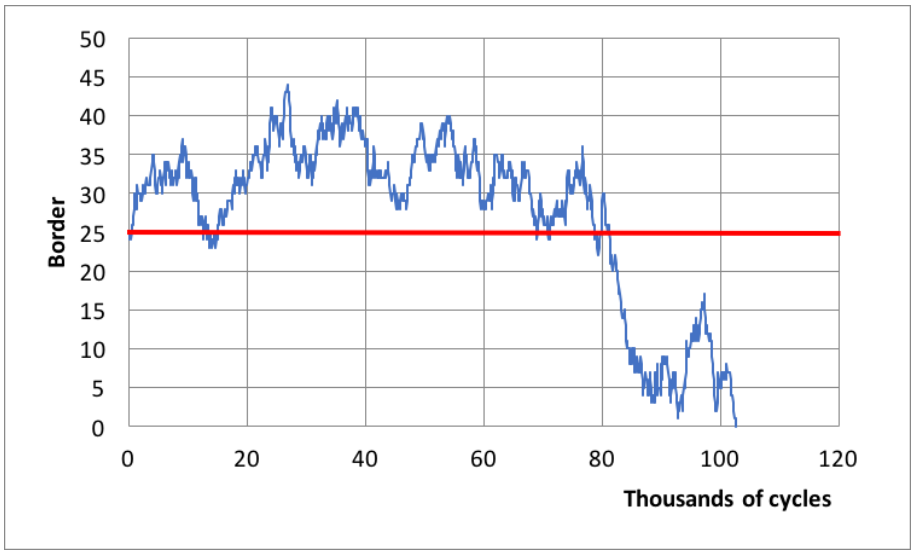

Figure S2. Example of border incursions in one replication with initially 75 Modern bands and 25 Neanderthal bands, with neutral drift (Modern fitness of .5). In this case, the Neanderthal incursion index registers 612,486 before eventual Modern fixation.

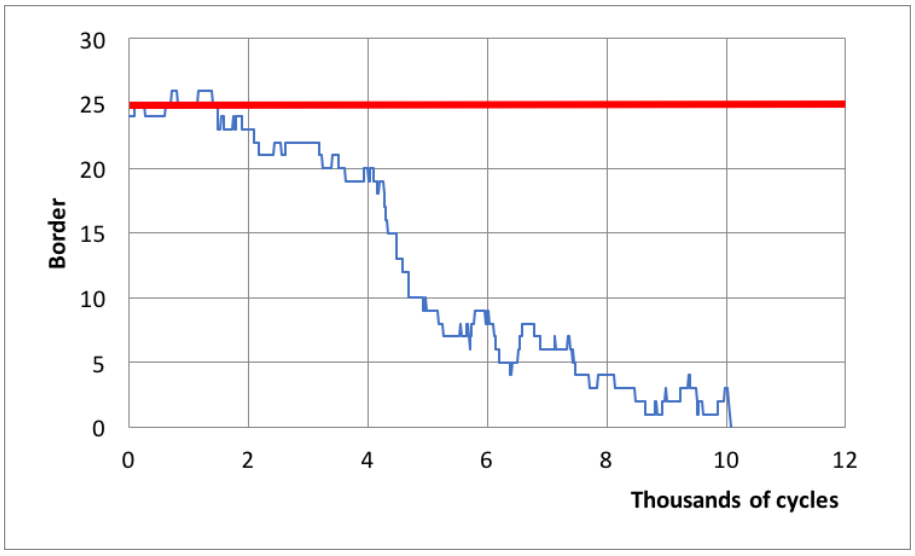

Figure S3. Example of border incursions in one replication with initially 75 Modern bands and 25 Neanderthal bands, with Modern fitness of .6. In this replication, the Neanderthal incursion index registers only 343 before Modern fixation.

Results in the main paper focus on a larger, more systematic experiment using these techniques to study paths to replacement.

3. Speciation, competitive exclusion, interbreeding, and genetic assimilation

Much of the Neanderthal replacement debate currently revolves around issues of speciation, regardless of whether this is made explicit. To some, the implication of interbreeding and Neanderthal genetic presence in modern Europeans is that the issue of replacement is misguided; Neanderthals and Moderns are populations of a single species. Therefore, it is useful to examine the grounds on which Neanderthals are classified as a separate species.

Speciation is a critical process in biological evolution. Although defining species is somewhat arbitrary, the biological features that classification seeks to understand are real [7]. Biological realities underlying species classification in sexually reproducing organisms are concerned with clusters of genotypic and phenotypic similarity, referred to as clades – groupings that include a common ancestor and all the descendants of that ancestor. These clusters arise out of accumulated mutations during a sufficiently long period of reproductive isolation, typically the result of geographic separation [1]. Members of the same species are more similar to each other within these clusters than to members of another species. Standard deviations of genotypic and phenotypic characteristics are greater between than within two species. A great deal of research has identified morphological and genetic traits held in common amongst Neanderthals that lie outside the scope of modern human variation. For morphological traits, see [8–14]. For genetics, see [15–23].

It is important to note that the capacity for viable sexual reproduction is no longer used to define species in the biological sciences [1,7]. Wolves and coyotes are well-studied cases, among many others, of viable inter-species reproduction [24]. Applying contemporary, cladistic biological standards, it is reasonable to classify Neanderthals and Moderns as two different, albeit very closely related, species. Because species-level fitness can be calculated as the average replication frequency across species members, the probability that this average would be identical for two different species exploiting similar niches (Neanderthals and Moderns) seems very low. As our models demonstrate, only a slight deviation from equal fitness is sufficient to result in reliable and rapid species replacement.

Fitness-based competitive exclusion leading to replacement by an invasive, and sometimes very closely related species is common and well-observed in the biological sciences [25–31]. Furthermore, competitive exclusion-based extinction between same-genus species frequently includes hybridization (interbreeding) and genetic pollution/swamping [31,32]. In other words, the presence of interbreeding does not, by itself, indicate pure drift. The assertion that Neanderthals are ancestors of modern humans, or are themselves modern humans, rather than an extinct branch of the same genus, is incorrect if made on the grounds of interbreeding alone. Neanderthals are ancestral and/or not extinct insofar as some of their genetic material persists, but this is

inconsistent with consensus definitions of ancestral species and extinction in biology. A fitness difference leading to a combination of competitive exclusion and genetic pollution via hybridization would place Neanderthal replacement in the company of a multitude of well-observed species replacement events. Explicitly, an assimilation hypothesis for Neanderthal replacement [33,34], resulting in a small amount of Neanderthal DNA in the subsequent population, bears the signatures of replacement via differential fitness.

4. Array based models

To examine our assumption of a relatively narrow zone of contact between Neanderthals and Moderns, we adapt our SBS model from a one dimensional vector to a two dimensional array. This is similar to two dimensional stepping-stone models, which have also been studied by probability theorists as *voter models on lattices*. We keep the total number of bands constant at 100, but vary how widely these are distributed. Specifically, we consider simulation widths of 1 (which reduces to our original model), 2, 5, and 10 (a square lattice). Finally, we keep fitness constant between the two types.

Figure S4 shows that simulation width has no effect on fixation probability. At drift, which species reaches fixation is once again a coin flip. However, Figure S5 shows that when the zone of contact between Neanderthals and Moderns is wider, fixation may occur much more rapidly than in a one dimensional vector. This is consistent with classic voter model findings, which suggest that fixation time should scale with n^2 in one dimensional cases, but with $n\ln(n)$ in square lattices (the 10 width case), where n is the total number of bands [35].

Finally, we show how the incursion index changes with simulation width in Figure S6. Note that, because we keep the number of bands constant, increasing simulation width results in a corresponding decrease in simulation depth (i.e., the depth of Neanderthal and Modern territory). However, bands presumably occupy the same geographical range in all cases. We therefore normalize the incursion index by dividing it by simulation depth. Doing so, we find that increasing simulation width increases the amount of Neanderthal incursions into territory initially occupied by Moderns.

In sum, fixation probability is invariant to assumptions about the relative width of the zone of contact between Neanderthals and Moderns. However, replacement may occur more quickly than in our one dimensional model when this zone is wide. Nevertheless, the number of Neanderthal incursions into Modern territory is equal to or greater than our original model, where incursions were already substantial under drift. As a result, while a wide array can achieve drift-based replacement in a realistic timeframe, the uncertainty of fixation and level of Neanderthal incursions into Modern territory under these conditions continues to present a poor fit with current archaeological evidence.

Regarding the most appropriate array width for stepping-stone models, we believe that a vector or very narrow array is most consistent with geographical constraints. In modeling total replacement/extinction over a long time span, it is important that we include the full depth of species' populations and territories, and not just their zone of interaction. At any

given snapshot in time, only a small percentage of total global Modern and Neanderthal populations would be interacting or in close physical proximity. To achieve replacement, a species must completely penetrate the full depth of the replaced species' initial territory. The estimated walking distance from the supposed origin of Moderns, up through the Levant and into Europe to Gibraltar is about 15,148 km. The widest part of Europe on that route is only about 946 km. Thus, the length is about .96 and the width in Europe is about .04 of the sum of those distances. Moreover, the Levant section contains two very narrow passageways. Neanderthal sites in the Levant (at Amud and Tabun, in contemporary Israel) are close to the Mediterranean coast. And the land passage between the Dead and Mediterranean Seas at contemporary Istanbul is only about 37 km. Perhaps the most suitable model would be a vector that is replicated numerous times to reach various different European locations at different times. Our vector simulation is replicated many times in each experimental condition. It is easy to imagine that empirical analogs could have reached different destinations across Europe with varying departure and arrival times over the 8 to 10 thousand years of inter-species contact.

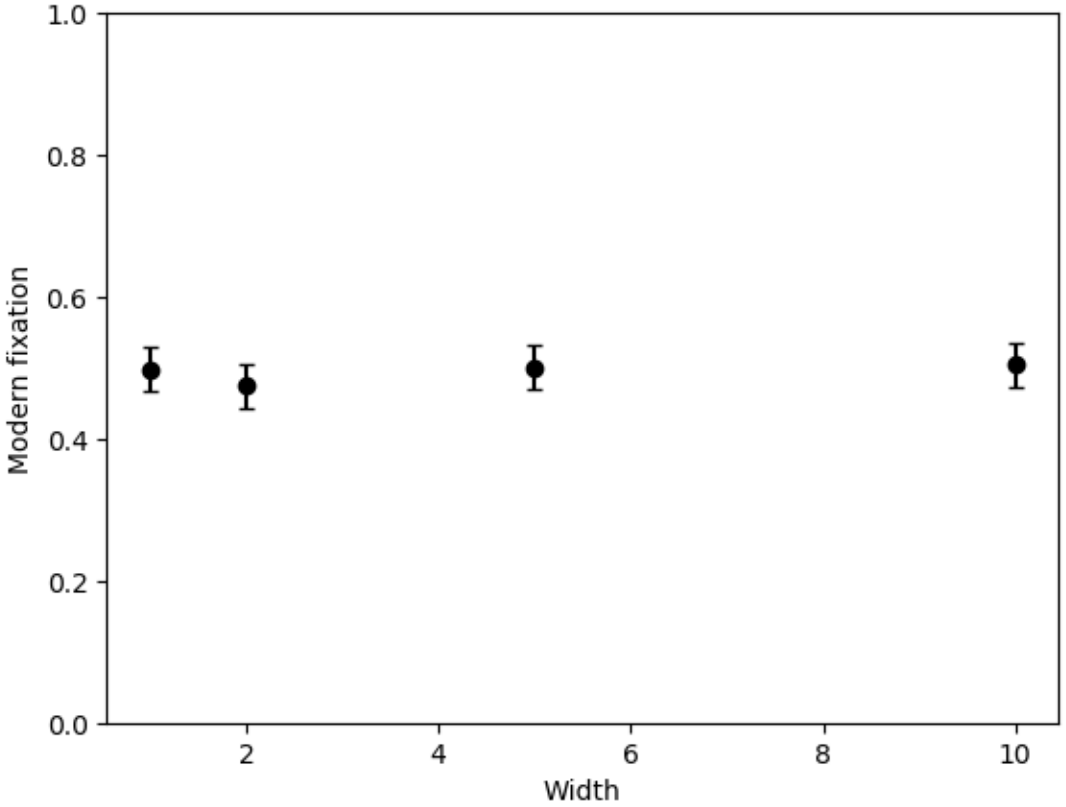

Figure S4. Effect of simulation width on Modern fixation. Increased width has no effect on fixation probability. Error bars reflect 95% confidence intervals.

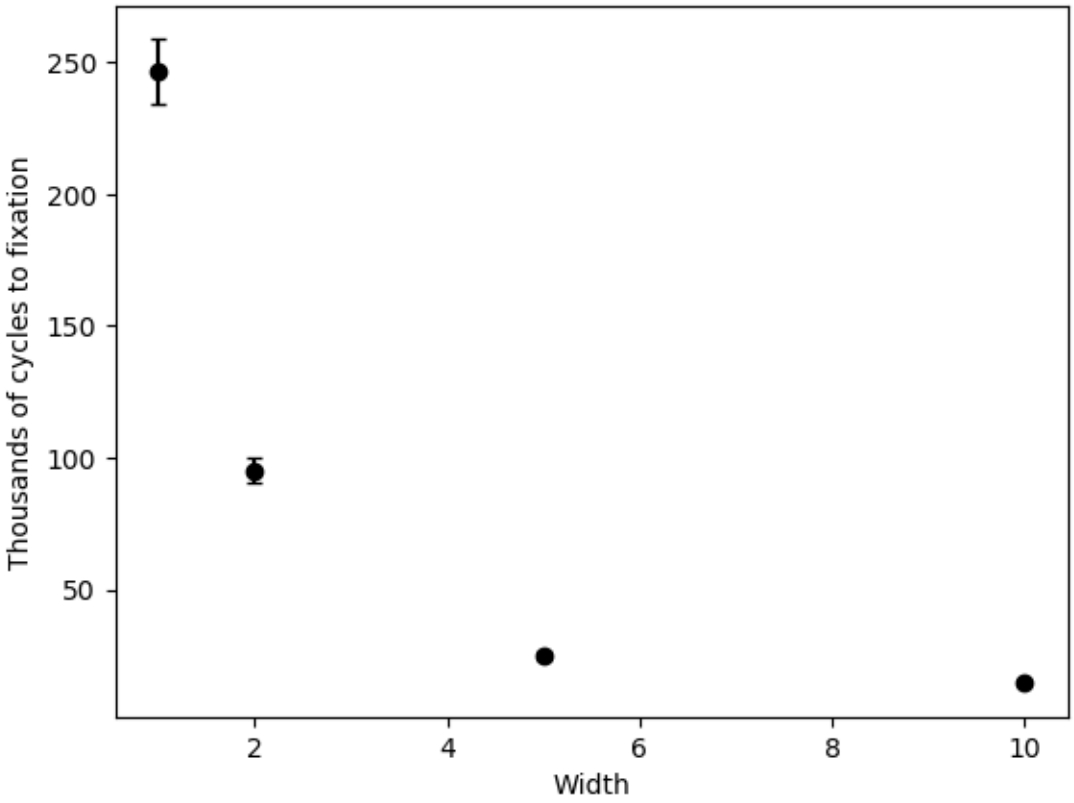

Figure S5. Effect of simulation width on number of cycles to fixation. When the zone of contact between Neanderthals and Moderns is wider, fixation is faster. Error bars reflect 95% confidence intervals.

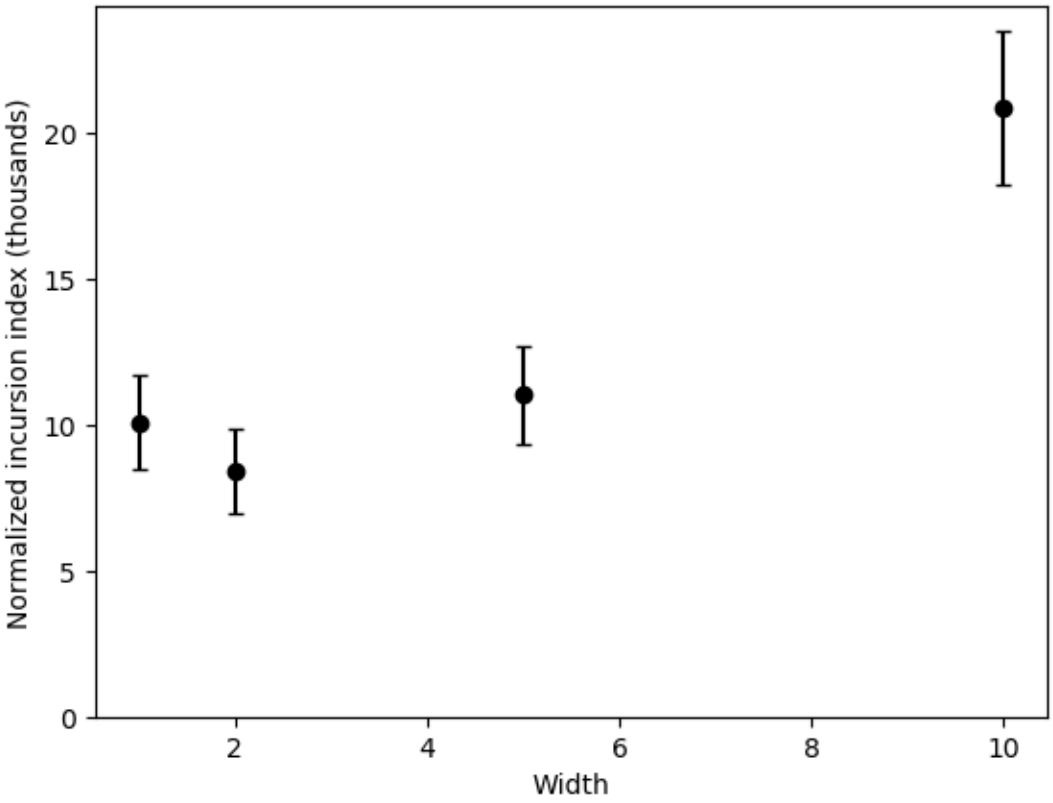

Figure S6. Effect of simulation width on incursion index, normalized by dividing by simulation depth. Increased width leads to greater incursion of territory initially belonging to Moderns. Error bars reflect 95% confidence intervals.

5. Analytical predictions using random walks

Our stochastic simulation model represents a series of discrete agents (i.e. bands) on a one-dimensional vector. However, because bands are represented solely as members of a given type (Moderns or Neanderthals), a meaningful change only occurs when a band is replaced by a band of another type. Although all band deaths and replacements are recorded, only movement of the border between Modern and Neanderthal populations is significant for species replacement. As a result, replacement can be represented as a random walk of this border. Throughout this paper, we plot simulation results against analytical predictions made on the basis of such random walks. To move between these analytical predictions and our SBS simulations, we need only convert time scales. We do so by observing that the border moves at each cycle with probability equal to death rate, $r = 0.01$.

In this section, we reinterpret group-level competition between Neanderthals (N) and Moderns (M) as a one-dimensional random walk of the border between the two types. Let ω_N be the fitness of Neanderthals and ω_M be the fitness of Moderns, where the fitness of each type falls between 0 and 1, and $\omega_N + \omega_M = 1$. Next, let λ be the total number of bands and b the position of the border between Neanderthals and Moderns, such that $0 \leq b \leq \lambda$. We take $b = 0$ as an absorbing state where Neanderthals have gone extinct and Moderns have reached fixation, and define $Pr(M)$ as the probability of reaching this state. This leaves $b = \lambda$ as an absorbing state where Moderns have gone extinct and Neanderthals have reached fixation, and we define $Pr(N)$ as the probability of reaching this state. Note that the position of the border b also represents the number of Neanderthal bands in the population. The number of Modern bands is therefore $\lambda - b$.

This section is divided into four parts. In the first, we derive the probability of a given type reaching fixation, which is equivalent to the common derivation of the probability of reaching a given absorbing state in a random walk. In the second part, we derive the expected number of steps to fixation, which is equivalent to the common derivation of the expected number of steps to absorption in a random walk. In the third part, we derive the expected amount of incursion by Neanderthals into Modern territory following initial contact, which corresponds to the incursion index discussed in the main text. Finally, in the fourth part, we derive the expected amount of time Neanderthals spend in Modern territory, given that Moderns reach fixation.

Probability of fixation

Let $Pr(N|b)$ be the probability of Neanderthals reaching fixation, given that the border (or total number of Neanderthal bands) is b. At any b, $Pr(N|b)$ is given by the product of $Pr(N|b+1)$ and the probability of the border moving to the right (ω_N), plus the product of $Pr(N|b-1)$ and the probability of the border moving to the left ($\omega_M = 1 - \omega_N$). This yields a recurrence relation

$$Pr(N|b) = (1 - \omega_N)Pr(N|b-1) + \omega_N Pr(N|b+1), \tag{S1}$$

which has a known family of solutions:

$$Pr(N|b) = c_1 \left(\frac{1}{\omega_N} - 1 \right)^b + c_2. \tag{S2}$$

Neanderthals have gone extinct when $b = 0$, so $Pr(N|0) = 0$. Conversely, Neanderthals have reached fixation when $b = \lambda$, so $Pr(N|\lambda) = 1$. Substituting these values into Equation S2 creates a system of equations. Solving it gives the fixation probability:

$$Pr(N|b) = \frac{\left(\frac{1-\omega_N}{\omega_N} \right)^b - 1}{\left(\frac{1-\omega_N}{\omega_N} \right)^\lambda - 1}. \tag{S3}$$

We can make several observations. First, this function is sigmoidal over $0 \leq \omega_N \leq 1$. It has a single discontinuity at $\omega_N = 1/2$, where fitness of the two types is equal, and so we must derive a separate solution for the case of drift. Finally, as the total number of bands increases, so too does the function's steepness (growth rate between asymptotes).

The probability of fixation at drift is given by setting $w_N = 1/2$ in the initial recurrence relation (Equation S1), and then repeating the derivation:

$$Pr(N|b) = \frac{b}{\lambda}. \tag{S4}$$

Because the probability of Moderns reaching fixation is $1 - Pr(N|b)$, we observe that, at drift, the probability of a given type reaching fixation is equal to the initial proportion of bands of that type.

Steps to fixation

Let $s(b)$ be the expected number of steps (movements of the border) needed to reach fixation, when starting from position b. At any given b, $s(b)$ is given by the recurrence relation

$$s(b) = 1 + (1 - \omega_N)s(b-1) + \omega_N s(b+1), \tag{S5}$$

where 1 represents the single step needed to move from this position, $\omega_M = 1 - \omega_N$ is the probability of moving to the left, $s(b-1)$ is the expected number of steps to fixation from $b-1$, ω_N is the probability of moving to the right, and $s(b+1)$ is the expected number of steps to fixation from $b+1$. This recurrence has a known family of solutions:

$$s(b) = \frac{b}{1-2\omega_N} + \frac{\omega_N}{(1-2\omega_N)^2} + c_1 \left(\frac{1-\omega_N}{\omega_N} \right)^b + c_2. \tag{S6}$$

No more steps can be taken when a type reaches fixation, so $s(0) = 0$ and $s(\lambda) = 0$. Substituting these values into Equation S6 creates a system of equations. Solving it gives the expected number of steps:

$$s(b) = \frac{b}{1-2\omega_N} - \left(\frac{\lambda}{1-2\omega_N}\right)\left[\frac{\left(\frac{1-\omega_N}{\omega_N}\right)^b - 1}{\left(\frac{1-\omega_N}{\omega_N}\right)^\lambda - 1}\right]. \tag{S7}$$

How does this value grow with the total number of bands? There are two cases to consider. In the first, Modern fitness exceeds Neanderthal fitness, and so the fitness ratio $(1-\omega_N)/\omega_N > 1$. This ratio gets very large when raised to the power of b or λ, and so we can safely ignore the constant -1 in the bracketed term. That term then simplifies to

$$\left[\frac{\omega_N}{1-\omega_N}\right]^{\lambda-b}, \tag{S8}$$

which rapidly approaches 0 as the number of Modern bands $(\lambda - b)$ gets large. As a result, only the first term in Equation S7 remains

$$s(b) \sim \frac{b}{1-2\omega_N}, \tag{S9}$$

and so the expected number of steps grows linearly with b, the initial number of Neanderthal bands. In the second case, Neanderthal fitness exceeds Modern fitness, which means that the fitness ratio $(1-\omega_N)/\omega_N < 1$. When raised to the power of b or λ, this ratio rapidly approaches 0, causing the bracketed term to become $-1/-1 = 1$. Removing it from Equation S7 and then simplifying gives

$$s(b) \sim \frac{\lambda - b}{2\omega_N - 1}, \tag{S10}$$

and so the expected number of steps grows linearly with $\lambda - b$, the inital number of Modern bands. If we assume that the initial population ratio (b/λ) remains constant, then in both cases the expected to number of steps grows linearly with the total number of bands.

To find the expected number of steps at drift, we set $w_N = 1/2$ in the initial recurrence relation (Equation S5), and then repeat the derivation:

$$s(b) = b(\lambda - b). \tag{S11}$$

We find that, at pure drift, the expected number of steps is a product of the number of bands of each type. Assuming an initially equal number of Neanderthal and Modern bands, the expected time to fixation is the square of one half the total number of bands. Note that, for both fitness and drift, converting from steps to simulation cycles merely requires dividing $s(b)$ by the death rate r.

Incursion amount

One empirically-relevant measure we propose to help distinguish between drift and fitness explanations is the amount of incursion into Modern territory that occurs once the two types meet. An incursion is characterized by both its depth into Modern territory and its duration. We calculate the total amount of incursion as a sum of each incursion's depth multiplied by its duration.

We begin by deriving $v(x|M)$, the expected number of times that a position x in Modern territory will be visited by Neanderthals from a starting position b, given that Moderns reach fixation. If we assume that x is visited exactly once before Modern fixation is achieved, then we can make a few observations. First, $b < x$, because Neanderthals occupy the left side of the vector while Moderns occupy the right. Second, x must be reached before 0, because 0 is an absorbing state where Moderns have reached fixation. Third, after reaching x, the border must move left and never return to x, because moving right would imply crossing x a second time to reach 0. The probability of reaching x from b exactly once before Modern fixation is therefore

$$\frac{Pr(x|b)\omega_M\overline{Pr}(x|x-1)}{Pr(M|b)}, \tag{S12}$$

where $Pr(x|b)$ is the probability of reaching x from b before being absorbed by state 0, ω_M is the probability of moving left from position x, $\overline{Pr}(x|x-1)$ is the probability of reaching absorbing state 0 from $x-1$ without ever returning to x, and $Pr(M|b)$ is the probability of Modern fixation. The number of times we expect to visit x once before Modern fixation is equal to the above probability:

$$v_1(x|M) = \frac{Pr(x|b)\omega_M\overline{Pr}(x|x-1)}{Pr(M|b)}. \tag{S13}$$

If the border reaches position x twice before Modern fixation, then one of two additional things must happen before x is left for good: Either the border must move left to $x-1$ (with probability ω_M), and end up back at x before Modern fixation; or the border must move right to $x+1$ (with probability ω_N), and end up back at x without Neanderthals reaching fixation. Therefore, once we are at x, the probability of reaching x again is:

$$\omega_M Pr(x|x-1) + \omega_N Pr(x|x+1). \tag{S14}$$

Taken together, the probability of reaching x from b exactly twice before Modern fixation is

$$\frac{Pr(x|b)\omega_M\overline{Pr}(x|x-1)\big(\omega_M Pr(x|x-1) + \omega_N Pr(x|x+1)\big)}{Pr(M|b)}, \tag{S15}$$

which is just a product of the probability of reaching x once before Modern fixation (Equation S12) and the probability of returning to x once after having reached it (Equation S14). To

get the expected number of visits to x as a result of passing through x exactly twice, we multiply the probability given in Equation S15 by the number of visits, two:

$$v_2(x|M) = \frac{2Pr(x|b)\omega_M\overline{Pr}(x|x-1)\big(\omega_M Pr(x|x-1) + \omega_N Pr(x|x+1)\big)}{Pr(M|b)}. \tag{S16}$$

From here, it is apparent that we can generalize this reasoning to any number of visits to x. The probability of reaching x exactly i times before Modern fixation is

$$\frac{Pr(x|b)\omega_M\overline{Pr}(x|x-1)\big(\omega_M Pr(x|x-1) + \omega_N Pr(x|x+1)\big)^{i-1}}{Pr(M|b)}, \tag{S17}$$

and the expected number of visits to x as a result of passing through x exactly i times is:

$$v_i(x|M) = \frac{iPr(x|b)\omega_M\overline{Pr}(x|x-1)\big(\omega_M Pr(x|x-1) + \omega_N Pr(x|x+1)\big)^{i-1}}{Pr(M|b)}. \tag{S18}$$

We can describe the total expected number of visits to state x using an infinite sum over i, where we add up the expected number of visits to x for every i:

$$\begin{aligned} v(x|M) &= \sum_{i=1}^{\infty} v_i(x|M) \\ &= \sum_{i=1}^{\infty} \frac{iPr(x|b)\omega_M\overline{Pr}(x|x-1)\big(\omega_M Pr(x|x-1) + \omega_N Pr(x|x+1)\big)^{i-1}}{Pr(M|b)}. \end{aligned} \tag{S19}$$

This expression can be rewritten as

$$v(x|M) = \frac{Pr(x|b)\omega_M\overline{Pr}(x|x-1)}{Pr(M|b)} \sum_{i=0}^{\infty} (i+1)\big(\omega_M Pr(x|x-1) + \omega_N Pr(x|x+1)\big)^{i}, \tag{S20}$$

where the infinite sum has a nice solution:

$$\frac{1}{\big(1 - \omega_M Pr(x|x-1) - \omega_N Pr(x|x+1)\big)^2}. \tag{S21}$$

The expected number of visits to x from b, before Moderns reach fixation, is therefore:

$$v(x|M) = \frac{Pr(x|b)\omega_M\overline{Pr}(x|x-1)}{Pr(M|b)\big(1 - \omega_M Pr(x|x-1) - \omega_N Pr(x|x+1)\big)^2}. \tag{S22}$$

To put Equation S22 in a usable form, we next solve for all of the conditional probabilities. For notational convenience, let γ represent the fitness ratio $(1-\omega_N)/\omega_N$. First, we can infer

from our solution for fixation probability (Equation S3) that the probability of reaching x from b is:

$$Pr(x|b) = \frac{\gamma^b - 1}{\gamma^x - 1}. \tag{S23}$$

Similarly, the probability of reaching x from $x-1$, without being absorbed by state 0, is

$$Pr(x|x-1) = \frac{\gamma^{x-1} - 1}{\gamma^x - 1}, \tag{S24}$$

which entails that the probability of reaching state 0 from $x-1$, without ever revisiting x, is:

$$\overline{Pr}(x|x-1) = 1 - \frac{\gamma^{x-1} - 1}{\gamma^x - 1}. \tag{S25}$$

Finally, the probability of reaching x from $x+1$, without being absorbed by state λ, is:

$$Pr(x|x+1) = 1 - \frac{\gamma - 1}{\gamma^{\lambda - x} - 1}. \tag{S26}$$

Replacing these solutions (as well as the probability of Modern fixation) into Equation S22 and simplifying gives:

$$v(x|M) = \frac{(\gamma+1)(\gamma^b - 1)(\gamma^\lambda - \gamma^x)^2}{\gamma^x(\gamma-1)(\gamma^\lambda - 1)(\gamma^\lambda - \gamma^b)}. \tag{S27}$$

Finally, we can combine the expected number of visits to each state, $v(x|M)$, with the depth of every such incursion into Modern territory, $d(x)$. Note that the depth of an incursion is simply the distance between x and the initial border b:

$$d(x) = x - b. \tag{S28}$$

Multiplying these values together gives the expected amount of incursion across the initial border b:

$$a(b) = \sum_{x=b+1}^{\lambda-1} v(x|M)d(x). \tag{S29}$$

Replacing in Equations S27 and S28, and then simplifying gives:

$$a(b) = \frac{(\gamma+1)(\gamma^b - 1)}{(\gamma-1)(\gamma^\lambda - 1)(\gamma^\lambda - \gamma^b)} \sum_{x=b+1}^{\lambda-1} \frac{(\gamma^\lambda - \gamma^x)^2(x-b)}{\gamma^x}. \tag{S30}$$

Solving the finite sum gives

$$\frac{\gamma^{2\lambda+1} + \gamma^{2b+1} - \gamma^{\lambda+b}((\gamma-1)^2(\lambda-b)^2 + 2\gamma)}{\gamma^b(\gamma-1)^2}, \tag{S31}$$

which we replace back into Equation S30, and then simplify to arrive at our final expression:

$$a(b) = \frac{(\gamma+1)(\gamma^b-1)\left(\gamma^{\lambda+b}((\gamma-1)^2(\lambda-b)^2+2\gamma)-\gamma^{2\lambda+1}-\gamma^{2b+1}\right)}{\gamma^b(\gamma-1)^3(\gamma^\lambda-1)(\gamma^b-\gamma^\lambda)}. \tag{S32}$$

However, when fitness of the two types is equal, this expression is undefined.

To get $a(b)$ in the case of drift, we substitute $\omega_N = \omega_M = 1/2$ into Equation S22, along with conditional probabilities inferred from Equation S4. This yields

$$v(x|M) = \frac{2b(\lambda-x)^2}{\lambda(\lambda-b)}, \tag{S33}$$

and:

$$a(b) = \frac{b(\lambda-b)(\lambda-b-1)(\lambda-b+1)}{6\lambda}. \tag{S34}$$

Note that, for both fitness and drift, converting from incursion amount to incursion index in the simulation requires dividing $a(b)$ by the death rate r.

Time spent in Modern territory

Let $t(x|M)$ be the expected number of steps Neanderthals will spend at position x in Modern territory, given that Moderns reach fixation and that the initial border is at b. Note that when the border moves right to x, all territory left of x is still occupied by Neanderthals. The amount of time spent by Neanderthals at x is therefore not equal to the number of visits to x, $v(x|M)$, but rather to the total number of visits to any position right of x (including x):

$$t(x|M) = \sum_{i=x}^{\lambda-1} v(i|M) \tag{S35}$$

Applying our solution for $v(x|M)$ from Equation S27, solving the finite sum, and then simplifying gives:

$$t(x|M) = \frac{(\gamma^b-1)((\gamma+1)(\gamma^{2\lambda+1}-\gamma^{2x})-\gamma^{\lambda+x}(\gamma^2-1)(2\lambda-2x+1))}{\gamma^x(\gamma^\lambda-1)(\gamma^\lambda-\gamma^b)(\gamma-1)^2} \tag{S36}$$

However, this expression is undefined when fitness of the two types is equal, and so we must repeat this process for drift by applying Equation S33 instead. Doing so, solving the finite sum, and then simplifying gives:

$$t(x|M) = \frac{b(\lambda-x)(\lambda-x+1)(2\lambda-2x+1)}{3\lambda(\lambda-b)}. \tag{S37}$$

Once again, converting from steps to simulation cycles requires dividing $t(x|M)$ by the death rate r.

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