The Neanderthal Extinction

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Abstract

Extinction and evolution are two sides of the same coin. When one creature disappears from the fossil record, we speak of "extinction" but there are multiple explanations for this phenomenon. During the emergence of the human species, a lot of our evolutionary "relatives" did not survive to this day. The Neanderthal is believed to be not only one of the most closely related hominins, but also one of the hominins that survived until most recently. In this essay I study different causes for the Neanderthal extinction, and consider whether it is likely that Neanderthals were absorbed in the human population of the time (anatomically modern humans, or AMH), or if humans replaced them. Considering the evidence for a large scale intermixture of Neanderthals an AMH is scarce, Neanderthals were most likely replaced by humans. What caused the Neanderthals to die out, and did AMH cause this event? And if AMH did not cause the Neanderthal extinction, how did the AMH, a very similar creature, manage to survive? While no large unified explanation can be given, it seems that a number of natural causes, including climate change and the inability of Neanderthals to adapt to them and the arrival of AMH have pushed the Neanderthal over the edge.

Contents

Introduction

During the existence of our planet, millions of different organisms have evolved, resulting in the incredible range of species we can see today. From small, single-celled bacteria to gigantic wales, all are believed to be derived from a common ancestor. During this development, however, many other species went extinct. Extinction and evolution are two sides of the same coin. When one species disappears from the fossil record, we speak of "extinction" but there are multiple explanations for this phenomenon. A population of now extinct creatures could have evolved over the generations, and now there seems to be now evidence for two species being the same, even in both came from a single lineage in the same geographical area. Another explanation is that the extinct species did not fit its niche anymore, either by being excluded from it by another species or by the disappearance of the niche itself. A final explanation could even be that, when a closely related species entered the already occupied area, the two populations "merged" and found the adaptations of one of the groups advantageous, thus preserving a majority of their traits, resulting in a seemingly disappearance of the other species. Humans themselves (anatomically modern humans, or AMH) are estimated, through the dating of fossils from Ethiopia, to have gotten into play at 195±5 ka (ka=1000 years ago) (McDougall et al., 2005) and are now the most abundant primate on the planet.

Figure 1. the distribution of different species of hominin. The vertical distance reports time and the different colors indicate the distribution(light-blue, West-Asia; green, Indonesia, dark-blue, Europe; red, Africa; pink, East-Asia). The manner of relatedness between different species is not shown in this figure. (Clive Finlayson, 2005)

The rise of the human species is no different from the emergence of other species in that many related species did not survive to this day. Of all hominin species only one has survived to this day, . One of our most related species, the Neanderthal, settled in Europa around 250 thousand years ago(KA), and has managed to survive, even though the last thousands of years only in isolated areas, until 28 KA (Finlayson, 2004; Davies et al. 2006). Seeing that the AMH settled in Europe around 45 KA (Wells, et al. 2001; Underhill et al., 2001), this means that there is an overlap of as much as 15 thousand years in which Neanderthals and AMH occupied the same area and had the possibility of contact. Though the AMH managed to survive in this region, the Neanderthal did go extinct. By looking at different possible cause for the Neanderthal extinction, I hope to describe both the effect of man on its close relative. As well as, by finding a reason why such a similar species went extinct, make a possible prediction about our own future.
The exact phylogenetic distinction of the Neanderthal is disputed. Though consensus holds that Neanderthals were closely related to AMH, it is not completely clear how the Neanderthals should be classified. The question if Neanderthal should be named *Homo neanderthalensis* or *Homo sapiens neanderthalensis*, since multiple definitions of species exist, will be avoided in this essay and Neanderthals will be referred to as Neanderthals. Since one of the definitions of a species is that, if different individuals can interbreed they belong to the same species, the species distinction cannot be completely avoided. Should one of the conclusions be that Neanderthals and AMH did interbreed, this might shed some light on this issue.

A description of Neanderthals

Neanderthal build

Neanderthals were a large, stocky hominin with an average body mass that is about 10 to 13 kg higher when compared to the bodymass of upper Palaeolithic humans (Ruff et al.,1999). The postcranial part of the Neanderthal body displayed a high distinction of muscles and varying levels of robusticity, especially in the upper torso (Trinkhaus, 2000). Not only is this robusticity connected to high levels of biomechanical stress inducing activity, it is also possible that it is partly related to adaptation to colder climates (Pearson, 2000). Since Neanderthals habitat stretched from western Europe to western Asia, the temperature was significantly lower than on the African plains, and adaptations to lower temperatures were probably required for survival.

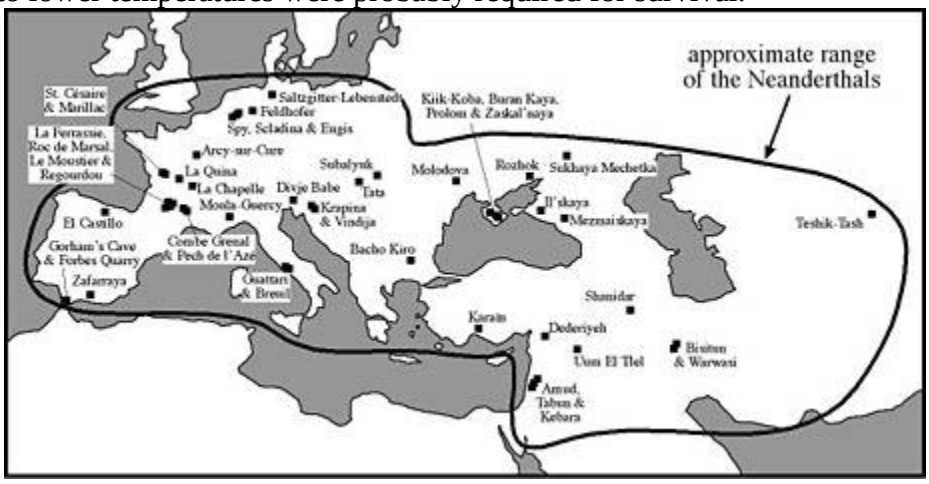

Figure 2. Neanderthal range and excavation sites in which Neanderthal remains were found.

It has been assumed that that the Neanderthal was adapted to a colder climate, since several other features seemed to be of a more “cold-resistant” form when compared to AMH. For example, the crural index, (the ratio of the length of the tibia to the length of the femur), of the Neanderthal is quite low when compared to the crural index of AMH, and therefore, following Allen’s rule (endotherms in colder climate will have shorter limbs when compared to an equivalent living in a warmer climate), a possible adaptation to inhabiting a colder climate (Howell, 1952). This trait however, falls within the variation found within the modern human population (Trinkhaus, 1981).

The large build of the Neanderthals resulted in a high basal metabolic rate. Added to this is the fact that both experimental studies and modeling show that Neanderthals’ shorter legs and burlier proportions increase the energetic cost for moving, resulting in a more expensive food acquirement (Trinkhaus, 2000; Weaver, 2005). The combination of these factors results in a higher amount of energy spent per day when compared to the extant hunter-gatherer populations.(Churchill, 2006; Steegman et al., 2000) On top of their already higher daily energy expenditure, it is possible that the energy required for the production and growth of offspring has been significantly higher than those for AMH.

Since not only the body size of the adult Neanderthals were larger than the AMH but they also grew at a higher pace, both the energy needed to carry a Neanderthal embryo to full term and the required energy to raise a Neanderthal child are expected to have been significantly higher.(Rozzi, 2004; Smith et al. 2007)

Food intake

Due to the fact that the nitrogen isotope ratios of the collagen of animal bones are between 3% to 5% higher than their dietary protein, the positions of organisms in food webs can be determined. By comparing different trophic levels, it can be determined that Neanderthals were toplevel predators. Plants during the Holocene in Europe mostly had δ15N levels of around 0 to 2%. Since the concentration in the bones of herbivores is higher (3 to 7%) and in carnivores another level higher at 6 to 12%, it is possible to discern the trophic level of an organism from the δ15N levels found in their bone collagen. Since the levels of δ15N in different Neanderthals was found to be between 8 and 12%, a fairly strong evidence is provided that at least a large part of their protein intake was dependent on the intake of meat (Richard and Trinkhaus, 2009). However, small remains in the dental calculi of Neanderthals also indicate that their diet was supplemented by a small amount of plants. (Henry et al. 2011)

Hunting habits

Neanderthal hunting would, in central and northern Europe, have operated on the open plains. The individual groups of Neanderthals were nomadic, but confined to smaller or medium distances (Conarda, Bolusc an Münzeld, 2012). The preferred target of their hunting parties seems to be large gregarious herbivores(such as horses or bisons) but there is also evidence for a smaller amount of other large game. (Conarda, Bolusc an Münzeld, 2012; Gamble 1999). Instead of killing with projectiles, the Neanderthal hunting group only engaged in direct contact with their prey, using lances instead of spears or bows and aided by beaters.(Gamble, 1999) There is no evidence found for a gender-divided split between hunters and gatherers, as both females and males partaking in the hunt (Kuhn and Stiner, 2006). This hunting structure could possibly cause a higher mortality when compared to (human) hunting groups using projectiles. (Trinkhaus, 1995)

Relationship with Humans

Though Neanderthals are considered to be one of the species that are the most closely related to the AMH. By looking at the difference between Neanderthal and sub-Saharan modern human genomes (more hominid species were included, but fall outside of the scope of this essay), it is possible to discern a timeframe for the population split between the ancestral population of both species. The time when this split happened is estimated to be between 275 and 765 KA (Prüfer et al., 2014; Green et al., 2010).

Interbreeding

Comparing the fossil record of humans and Neanderthals have shown no evidence for interbreeding between Neanderthals and an sub-Saharan AMH populations (Mellars, 2006). Even if Neanderthals did not inhabit sub-Saharan Africa, introgression of the Neanderthal genome into the sub-Saharan human genome could have happened before the ancestors of the Neanderthals have left Africa, however, genetic studies have found no detectable introgression (Christopher Wills, 2011). This suggest that, if there was introgression of the Neanderthal genome into the AMH genome, it could only have happened after the ancestral population of non-African humans have left Africa. One way to discern this is to test the differing relatedness between Neanderthals and both sub-Saharan African and non-African humans. It was found that not only are Neanderthals related more closely to non-Africans than to Africans, it is estimated that around 1.5 to 2.1% of the non-African nuclear genome is derived from the Neanderthal genome (Prüfer et al., 2014). There was, however, no evidence found for introgression the other way around, i.e. there does not seem to be human derived DNA in the Neanderthal genome (Green et al., 2010). For the mitochondrial DNA, it seems to be another fact entirely. There has been no evidence found for Neanderthal admixture to the mitochondrial genomes of AMH.

Not only was the genetic variation of Neanderthals quite low, reoccurring bottlenecks have caused a loss in genetic variation among AMH that migrated further out of Africa (Ramachandran et al., 2005). This reduction in genetic variation might have facilitated a persistence of Neanderthal DNA in AMH (and vice versa), because the influx of more variation could offset the otherwise lower variation of both populations. In populations with a higher amount of variation, this influx is more likely to decrease the fitness, since there is already a higher amount of variation for both good and neutral genes (Christopher Wills, 2011).

Habitual elements

Population size.

The autosomal genome of a Neanderthal from the Altaï mountains carries 1.7-1.8 heterozygous sites per 10.000 base pairs. When compared to the number of sites found in modern day human population, this seems between 70 and 84% lower (Prüfer et al. 2014). In this particular case, the Neanderthal had been the result of a history of inbreeding, which might not have been the case for other populations. However, when removing the effect of this inbreeding, the amount of heterozygous sites remains not only lower than in present-day humans, but is in fact amongst the lowest measured of any organism (Leffer et al., 2012). This low amount of heterozygous sites could indicate either an extremely strong selection on a high amount of the Neanderthal genome, or it could indicate a relatively small population size. By looking at the amount of time that has passed between the most recent common ancestor of the two copies of the genome a person caries it is possible to reconstruct the demographic history of a population. All genomes analyzed by Prüfer et al. show evidence for a decrease in population size around 1 million years ago. However, since then the population that resulted in the modern-day humans increased in size again, and the ancestral Neanderthal population continued to decrease in size. It should be noted that only a single Neanderthal was sequenced, so subsequent sequencing of other populations might offer a more certain assessment of the life-history of Neanderthals.

Different genetic studies have varying results concerning the population size of Neanderthal. For example, the effective population size, derived from nuclear DNA is expected to have been ranging between 3.000 and 12.000 individuals (Green et al. 2006). Most studies however have worked with mitochondrial DNA, and reached result varying from 1.476 to 32.000 individuals. (Ghirotto et al. 2011, Briggs et al. 2009). All studies agree however, that the effective population size has been fairly low.

Brain Diseases

Transmissible spongiform encephalopathy's (TSE's) are a group of diseases that are cause by prions, and that result in degenerative brain disorders. Of these TSE's multiple human-specific forms are known. There are 3 ways in which a human can become infected with a TSE: random folding mistakes in proteins, hereditary predisposition or getting into contact with infected tissue. (Belay, 1999) it is also found that some groups of Neanderthals practiced cannibalism, and it is possible that, when one infected Neanderthal got consumed, it infected those that fed on it. Not only the directly eating of infected tissue is a possible way to get TSE's, it is also possible that, through the stone tools the Neanderthals used, they infected other members indirectly. If TSE's had spread throughout the entire population, it is possible that sporadic emergences of them could exterminate different smaller groups, resulting in a strong reduction of the possibility of Neanderthals to adapt to changing conditions (Underdown, 2007)

Climate change

Food-availability

Fluctuations in climate could have had a discernable effect on the environment of the Neanderthal. During different era's, multiple climate cycles are found to have been in effect. Longer cycles (Heinreich events, 10-8 kyr) happened simultaneously with shorter cycles (Oeshger-Dansgaar events, 1.5 kyr). Since 130 KA 25 of these Oeshger-Dansgaar events have been known to have happened in Europe (Sanchez-Goni et al., 2008). These Oesherger-Dansgaar event have an effect on the availability of gregarious animals who make up the primary part of the Neanderthal diet. The possibility exists that Neanderthal groups followed the migrating animals, but considering the southern areas of Europe were already colonized by other groups, it is assumed that local extinctions, and later, during the warmer periods, recolonizations have occurred (Hublin and Roebroeks, 2009)

Direct survival problems

Neanderthals occupied a large portion of Europe, and their habitats covered multiple climates, ranging from cold or cool climates to temperate ones. Although their body proportions could be explained as morphological adaptations to the cold temperatures(Howell, 1952) it is possible that their stocky build is a result of technical limitations instead of a true genetic adaptation (Hublin, 2009). The Neanderthal do seem restricted in their ability to persist on a peri-artic landscape. Large parts of Europe were deserted and repopulated during several episodes such as OIS 6 and OIS 4 (OIS = oxygen isotope stages are alternating temperature periods in the earth's climate, deduced from oxygen isotope data that reflect changes in temperature).(Hublin, 1998; Hublin and Roebroeks, 2009). Recent models discovered that there seems to be little evidence supporting a wildly varying difference in cold resistance between Neanderthals and AMH (Sørensen, 2011).

Human-caused reasons

Instead of natural causes, the Neanderthal extinction might have happened because of human interaction.

Extinction of Megafauna

The fossil record shows that there have been multiple waves of extinction since the Pliocene that coincide with hominin dispersion. In the most cases of natural extinction, the species that become extinct is replaced by another, possibly related species. For these series of extinctions, however, no "replacement" has emerged. In Africa, where hominins and other native fauna had a long time to co-evolve, there have been no such extinctions observed. In other parts of the world, these major extinctions did happen. If they had happened because of a change in climate, it would be expected that when these extinctions happened, they would happen simultaneously over similar longitudes. As this is not the case however, there must have been another cause. Since these extinctions coincide with hominin expansion, the arrival of hominins are an plausible candidate. It is of importance, however, that hunting of these large animals is not the only possible cause of their extinction. The use of fire has likely also played a large part in this. It has been observed that the presence of hominins also corresponds to an increase in fires. The hominins, even if they were not capable of creating their own fire, are found to use and preserve naturally occurring fire (caused by lightning etc.). When these fires spun out of control, they could reduce a large part of the dry plains on which a large part of the Megafauna lived to ashes, severely reducing not only the amount of fauna present but also limiting their food source.

In Iberia, it is know that, while the amount of large mammals decreased, the amount of rabbits increase. Since rabbits were such an available food source, it would be expected that at least some of the Iberian predators shifted from prey. And while it is observed that other predators over time specialized on the rabbit hunt (Ferrer & Negro, 2004), Neanderthals did not show such a dramatic prey shift. Even though the mean weight of a prey show a decreasing trend, the amount of rabbit in the Neanderthal meal does not increase. One explanation for this observation could be that the rabbit would be too hard to find for the Neanderthals. Rabbits, however, occupy large, easily visible warrens were a large number of prey are present, making it a relatively safe and abundant resource. On the other hand, when AMH arrive in Iberia, the use of rabbits dramatically increases. Though the dependency on a single prey like rabbits might not be representable for the entire Neanderthal population, his indicates that, while AMH were able to shift to smaller prey when their larger counterparts disappeared, the Neanderthals seem to have been confined to the larger, increasingly spare, large prey (Fa et al., 2013).

Social differences

Even though Neanderthals and AMH had an overlap in their prey of choice, Neanderthals were divided in smaller groups, are suspected to have little to no contact with other Neanderthal groups (apart from mating). AMH on the other hand, had the possibility to maintain larger social networks with other groups (Adler et al., 2008). This habit does give AMH a considerable advantage, considering the fact that they might have more information about the location of the herds of their prey. Another advantage AMH would infer from more communication between different groups, is the possibility of trade. If different groups can specialize in different occupations, then the total efficiency of the population increases, and can even be greater than a similar population that had greater individual efficiency.

Discussion

There are multiple studies that show that Neanderthals and AMH have had a small amount of interbreeding. If the Neanderthal population "merged" with the AMH population of Europe, it is expected that Europeans show a higher amount of DNA that originated in Neanderthals. However, as the amount of Neanderthal DNA does not differ between Asian populations and European populations, the most likely explanation is that the interbreeding events happened shortly after the AMH left Africa. While this does provide a new point of view for the Out of Africa Hypothesis, I doubt that this interaction had a large part to play in the Neanderthal extinction, as large part of the Neanderthal population would have no interbreeding with AMH in this case. Further genetic studies might show the amount of human DNA in Neanderthal genomes, but to my knowledge, no such studies exist on the time of writing of this essay. On the other hand, there are also some studies that show no interbreeding between Neanderthals and AMH, which further indicates the fact that, when interbreeding happened, it happened a long time ago and in a low frequency. Combining these two standpoints does not seem likely that the Neanderthal and AMH population in Europe "merged", but that the extinction of Neanderthals was due to another reason.

Habitual procedures

The fact that Neanderthals were dependent on large game for their could prove to be a major handicap for them. Not only was hunting a difficult and dangerous task for the Neanderthals, with a high probability of injuries, the fact that they were so specialized in one kind of prey meant that, when those prey disappeared or declined in number, their food availability drastically reduced. Combined with the fact that Neanderthals do not seem to have been capable of (easily) shifting to smaller game, their choice of prey does seem like an impairment. The fact that their daily energy requirement was significantly higher than the AMH only strengthens this hardship.

Another Neanderthal habit that had negative long term effect was the act of cannibalism. While cannibalism can have short term advantages, there is also the danger of certain diseases, and when a group is persistent in the act of cannibalism, these can cause serious fitness impairments. In fact, in human groups where cannibalism is practiced for a longer period of time, a lot of diseases sweep through the community as well.

Population size

The smaller group size of Neanderthals could have also had a negative influence on their possibility to survive. Their smaller size of their groups made them more susceptible to a changing environment, since not only the variation within a small group was limited, the possibility of a small part of the group surviving a negative event also reduces. For example, if two populations were caught by surprise in a storm or similar event, and the odds of survival are 95% for each individual, a group of 10 individuals would likely die out completely (or have one member left) while a group of 100 individuals are expected to have around five survivors. This example is oversimplified, but it shows that a larger

group has a bigger chance of surviving such an event. The relatively isolated small groups in which the Neanderthals lived, could also have caused another disastrous process, in the form of genetic drift. In smaller populations, genetic drift has a much larger chance to fixate un-advantageous genes. This is most likely not an immediate problem, but can cause a both a loss of variation in the population and can even cause negative traits to become prevalent in the population over a larger amount of time.

Climate change

The habitual changes in climate during the Neanderthal occupation of Europe are also a major influence in the extinction of Neanderthals. These climate changes did not only decrease the availability of their primary food source, which by itself is already a major limiting factor, the decreases in temperature also diminished the portion of the land in which the Neanderthals persisted. While humans are at least the same amount and probably more susceptible to the colder climates, the invention of clothes made them able to spread out over a larger part of Europe and reduced the need to "escape" the cold fronts.

Human causes.

There is little evidence for a direct war-like competition between Neanderthals and AMH. However, as we observe the profound influence of humans on their environment, secondary effect are likely to have influenced the Neanderthal demise. The decline in megafauna, for example, while also influenced by climate change, is probably affected by the human expansion as well. Not only the hunting of AMH could cause this decrease, but the use of fire (either found or human-made) is also a likely suspect for the decrease of megafauna. Larger fires, if uncontrolled, could reduce a large part of drier plains to ashes, both killing larger animals directly and destroying their food source.

Another indirect factor caused by AMH is competitive exclusion. This theory states that, when two creatures occupy the same niche, only the most efficient can survive. Though Neanderthals and AMH did not occupy the same niche, there was an overlap in their food source. Considering the fact that AMH were much more efficient hunters, due to their use of projectile weapons, this seems like a likely possibility. The more sophisticated weaponry and larger numbers of the AMH population could also mean that they were endangered less by the larger predators that roamed Europe, and that they had the possibility to monopolize certain key areas, like watering holes.

Conclusion

The Neanderthal extinction can be attributed to a myriad of causes. The possibility of being absorbed in the human population, or even have interbreeding during the AMH occupation of Europe, does not seem to be a likely possibility. The most likely cause seems to be a combination of natural and human causes. A colder climate, a decrease in prey and arrival of AMH, combined with the inability of Neanderthals to change, could all, and probably have all had an impact on the amount of Neanderthals surviving. Considering the small, relatively isolated groups the Neanderthals lived in, it is also completely possible that all of these factors have caused a single group to die out. I believe that, had AMH not occupied Europe, the Neanderthals would still have died out, though it might have taken a longer time. For our own future, I would consider this a warning. It could very well be possible that there are certain conditions to which the humans species cannot adapt. In contrast with the Neanderthals however, I suspect these conditions to be more uniformly caused by ourselves then to be natural causes.

When looking at human evolution however, one cannot ignore the effect of innovation. These adaptations, through technological/cultural means, can effect a population immensely. Imagine for example, a world in which electricity or vaccination was not invented. This world would look dramatically different from our own. It might very well be possible that AMH discovered projectile weapons through sheer luck. The effect of these projectile weapons, however, would have a positive effect on the survival of humans. If, through more efficient hunting and longer life expectancy, the populations of humans began to grow in size, the chance that another "invention" that increased the possibility of survival was invented would increase, which would in its turn increase the chance for another "invention". Maybe, if Neanderthals had developed projectile weapons (or another kind of technology) they would have been able to survive, and maybe humans, it they didn't discover projectiles (or clothes, or later on farming etc.) could have gone extinct in their place.

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