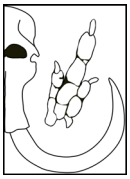
Fossilia, Volume 2018: 53-56



Small and isolated: ecology and fragmentation of Neanderthals

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Keywords:
Homo neanderthalensis;
Species distribution modelling;
fragmentation.

Bullet-Points Abstract

- *Homo sapien*s greater ecological plasticity allowed this species to react better to climate changes
- AMHs maintained a more continuous occupation of its potential habitat
- Habitat reduction and fragmentati*on in Homo neanderthal*ensis must have had dramatic consequences on its population size.

Introduction

Neanderthals lived in Eurasia alongside anatomically modern humans (AMHs). The oldest evidence of a Neanderthal population was found at Zuttiyeh (Israel), with an age around 200,000 years ago, Tabun (Mount Carmel, Israel) around 150,000 years (Grun et al., 1991) and Altamura (Italy) at around 150,000 years (Lari et al., 2015). Neanderthals present unique morphological characteristics that make them very different from AMHs. They had a large nasal cavity, reduced chin, and short limb proportions suggesting a limited stature (Helmuth, 1998). Moreover, Neanderthals had a wide chests and large lung volume (Franciscus & Churchill, 2002; Macias & Churchill, 2015). For years scientists considered these features as adaptions to cold climates. Higham and colleagues (2014) statistically placed the extinction of *Homo neanderthalensis* King, 1864 around 40 ka, almost in coincidence with Heinrich Event 4 (HE4). This event consists in a sudden and global shift towards colder temperatures (Van Meerbeeck et al., 2009).

It has been demonstrated that Neanderthal populations experienced major demographic contractions during the HE4 cold event in Northern Iberia and Southern France (d'Errico & Goñi 2003; Sepulchre et al., 2007). This evidence shows that, contrary to the previous assumptions, the Neanderthal is not an ice age species. There are different works that seem to support this hypothesis (Finlayson & Giles, 2000; Stewart, 2004; 2007; Bradtmöller et al., 2012).

The late contraction of *H. neanderthalensis* range to southern Europe coincides with the spread of AMHs, suggesting a possible instance for competitive exclusion between the two (Banks et al., 2008; Mellars & French, 2011). Negative interactions between Neanderthals and AMHs are often viewed as the potential drivers of *H. neanderthalensis* extinction, as an alternative to climate change hypothesis, or a combination of the two causes (Rey-Rodríguez et al., 2016).

Melchionna and colleagues (2018) used Species Distribution Modelling (SDM) to quantify and compare statistically the inferred climatic niches of *Homo sapiens* Linnaeus, 1758 and *H. neanderthalensis* in Western Eurasia during the last 8 ka of Neanderthals existence. The aim of that work was to evaluate the niche evolution

and overlap in the two species, identifying their optimal habitat patches and to which degree these patches connected to each other.

Materials and Methods

As first step, we used fossil occurrence records (the Stage Three Project archaeological database, van Andel, 2002; the Canadian Archaeological Radiocarbon Database, Gajewski et al., 2011; the Radiocarbon Palaeolithic Europe Database, Vermeersch, 2017) and paleoclimatic data (Singarayer & Valdes, 2010). Both fossil and archaeological occurrences were used. Only radiocarbon records computed by using Accelerator Mass Spectrometry (AMS) were taken into account. Dates were calibrated under the 'IntCal13' curve, by using the R package 'Bchron' (Parnell, 2016). The framework was divided in three different temporal windows, at 48 ka, 44 ka and 44 ka ago.

To model the potential distributions of *H. sapiens* and *H. neanderthalensis* we used Species Distribution Models (SDMs) These models allow to combine both occurrences and climatic information to compute the potential habitat of the species (Maiorano et al., 2013). The final product of this procedure is a suitability map. Suitability can be defined as a measure of how much the habitat is suitable for a species to occur in a given place and during a given time. The SDMs computation was performed under the R software environment.

After that, we evaluated the degree of structural con-

How to cite: Melchionna (2018). Small and isolated: ecology and fragmentation of Neanderthals. *Fossilia*, Volume 2018: 53-56. https://doi.org/10.32774/FosRepPal.20.1810.075356
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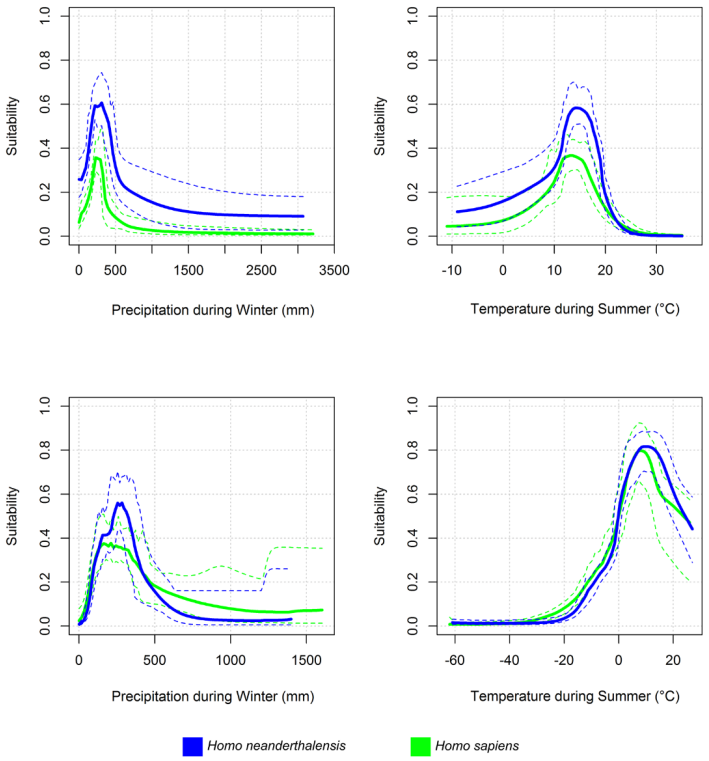

Fig. 1. Suitability analysis results. Response curves depict the variation of the probability of presence versus each variable. Blue (green) curves referring to *H. neanderthalensis* (*H. sapiens*). Dotted lines represent the range interval over the 100 SDMs run per species in order to account for dating uncertainty.

nectivity between optimal habitat patches as predicted by SDMs for the two species separately, focussing on different landscape metrics describing the number of Patches, their area and degree of connection.

Results and Discussions

The suitability analysis showed that Neanderthal suitability is higher for 3 out of 4 climatic predictors (Fig. 1), meaning that *H. neanderthalensis* was better than *H. sapiens* at his climatic optimum. This is not surprising, because Neanderthals originated in Eurasia, so they were well adapted to this climatic condition. Response curves of both species are highly overlapping, suggesting close similarity between Neanderthals' and AMH's potential climatic preferences. However, looking at the tails of the distribution, it can be noticed that *H. sapiens* curves offset those of *H. neanderthalensis* for three of four predictors, namely temperature during summer and both precipitation variables, suggesting a wider tolerance to these predictors for *H. sapiens* (Fig 1).

The connectivity analysis showed an increase in occupied patches toward the present, but in Neanderthals only, while the number of patches occupied by *H. sapiens* remains stable (Fig. 2, top). At the same time, the whole range of *H. neanderthalensis* decreases through the process. The patches occupied by Neanderthals thus became smaller and more isolated (Fig. 2, bottom). This is true especially for the 44 and the 40 ka temporal windows.

Our findings seem to confirm the hypothesis of a regional extinction model for North-Western Neanderthal populations in the coldest (Northern) stretches of its habitat (Hublin & Roebroeks, 2009), before the full spread of AMHs in Europe, placed around 42 ka (Benazzi et al., 2015). Benito et al. (2017) recently demonstrated *H. neanderthalensis* most suitable environment during the Eemian was the Mediterranean area, while mountain ranges and continental plains showed low habitat suitability. Our data strongly concur on these findings. Genetic and demographic data also are consistent with these notions. Neanderthals were found to have had small population size and high mortality rates (Trinkaus, 1995; Sørensen, 2011; Bocquet-Appel & Degioanni, 2013).

It appears clear that the climate change played a fundamental role in Neanderthals demise. At the same time, the presence of AMHs in Europe could have been limited the latest Neanderthal populations as well. However, a real process of habitat fragmentation occurred in the *H. neanderthalensis* population and it must have had dramatic consequences on its size.

Conclusions

Our findings show that *H. sapiens* had greater ecological plasticity over Neanderthals, which probably al-

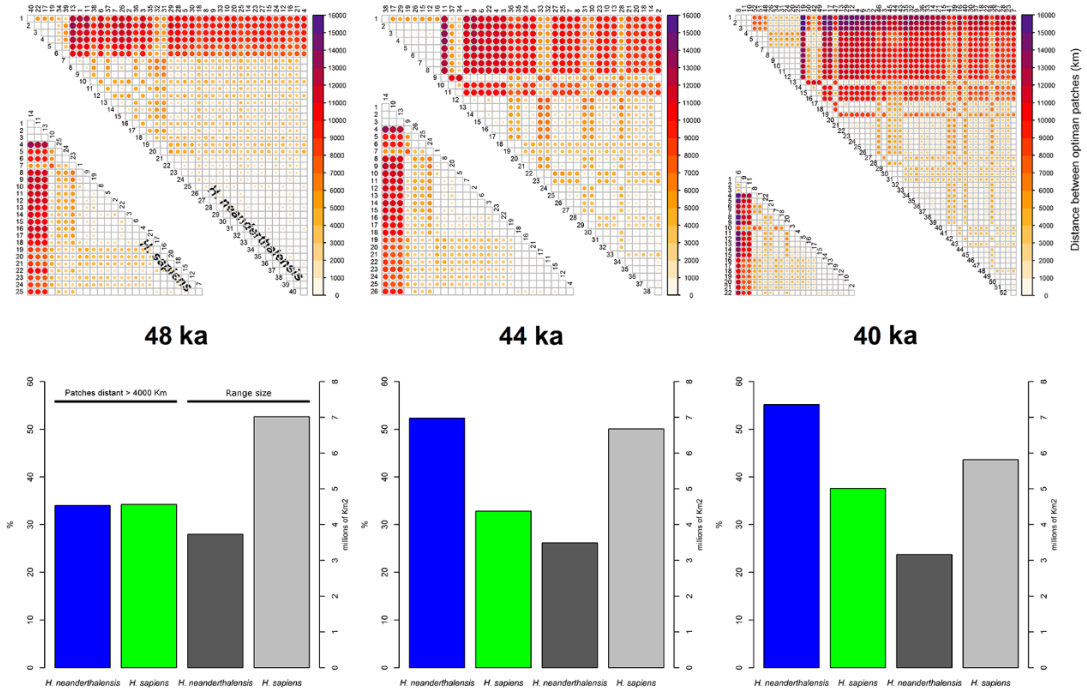

Fig. 2. Evolution of optimal habitats in Neanderthals and AMHs. Dots represent the linear distance in kilometers between optimal patches pairs (i.e. above the 95th percentile of the suitability values predicted by the ensemble forecasting). Distance increases from white to purple and is proportional to dots size. Row and column numbers refer to the individual patch ID. Blue (green) columns in bar plots summarize the percentage of optimal patches pairs >4000 km apart for H. neanderthalensis (H. sapiens) in the three time points. Dark grey (light grey) bars indicate range size of *H. neanderthalensis* (*H. sapiens*) in millions square kilometres.

lowed this species to better react to climatic worsening at 44 and then at 40 ka. On the contrary, Neanderthals potential habitat appear to be very reduced and fragmented during the last phase of their occupation. Moreover, habitat reduction and fragmentation in *H. neanderthalensis* suggest its population became unfit to recover in the wake of climatic change.

Acknowledgements

The author is grateful to Andrew Martindale for sharing with us the CARD data. Anna Loy provided important insights about the idea at the base of this study.

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Manuscript received 5 August 2018
Received after revision 16 October 2018
Accepted 22 October 2018