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Were Neanderthals responsible for their own extinction?

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ABSTRACT

After more than 100,000 years of evolutionary success in Western Eurasia, Neanderthals rapidly went extinct between 40,000 and 30,000 years ago, almost coinciding with the spread of Anatomically Modern *Homo sapiens* (AMHS) in Europe. Several scenarios relate their extinction to competition with AMHS, climatic changes during the last glacial period or a combination of both. Here we propose a much simpler scenario, in which the cannibalistic behaviour of Neanderthals may have played a major role in their eventual extinction. We show that this trait was selected as a common behaviour at moments of environmental or population stress. However, as soon as Neanderthals had to compete with another species that consumed the same resources (AMHS in this case) cannibalism had a negative impact, leading, in the end, to their extinction. To test this hypothesis, we used an agent-based model computer simulation. The model is simple, with only traits, behaviours and landscape features defined and with no attempt to re-create the exact landscape in which Neanderthals lived or their cultural characteristics. The basic agent of our system is a group of individuals that form a community. The most important state variable of our model is the location of the group, coupled with a defined home range and two additional factors: cannibalism and the chance of fission. The result of the simulation shows that cannibalistic behaviour is always selected when resources are scarce and clustered. However, when a non-cannibalistic species (late Pleistocene AMHS) is introduced into the same environment, the cannibalistic species retreats and the new species grows until it has reached the carrying capacity of the system. The cannibalistic populations that still survive are displaced from the richest areas, and live on the borders with arid zones, a situation which is remarkably similar to what we know about the end of the Neanderthals.

1. Introduction

Neanderthal extinction is one of the most widely debated topics in Eurasian prehistory. Most of the proposed scenarios in the past have related the extinction of the species with the spread of Anatomically Modern *Homo sapiens* (AMHS) throughout Europe. According to this scenario, AMHS would have benefited from some kind of cultural or biological advantage over Neanderthals (Pettitt, 2000; Hockett and Haws, 2005; Svodoba, 2005; Kuhn and Stiner, 2006). At the opposite extreme, other authors have proposed a purely climatic scenario in which Neanderthals retreated due to environmental changes, leaving an empty space in which AMHS flourished as a consequence of having less strict ecological restrictions (Finlayson, 2004; Finlayson and Carrion, 2007). An intermediate position proposes a mixed scenario in which the climatic oscillations of OIS 3 would have favoured the expansion of AMHS over that of Neanderthals (Mellars, 1998; d'Errico and Sanchez Goñi, 2003; Banks et al., 2008; Barton et al., 2011). In any case, all these scenarios are based on cultural, biological or climatic assumptions which are the subject of heated debate. Here we propose a much simpler scenario, taking into account only one of the traits that seems to characterize a number of Neanderthal populations: cannibalism.

Cannibalism has been documented in a number of Neanderthal sites: Kaprina (Russell, 1987; Patou-Mathis, 1997; White and Toth, 2007), level 25 from Combe Grenal (Garralda and Vandermeersch, 2000), Moula-Guercy (Defleur et al., 1999) Pradelles (Maureille et al., 2007), Cueva del Boquete de Zafarraya (Barroso et al., 2006), El Sidrón (Rosas et al., 2006). This behaviour has been also described in a number of hominin species, including *Homo*

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antecessor and *Homo rhodesiensis* (White, 1985; Fernández-Jalvo et al., 1996, 1999; Saladie et al., 2012). Through this study we aim to explore the importance of biological cannibalism (as opposed to cultural cannibalism). In particular, we want to determine the conditions in which this trait is positively selected and what happens when a second, non-cannibalistic group (in this case late Pleistocene AMHS) is added to the system. A computer simulation was used to test this scenario. This allowed us to create and experiment with scenarios in which environmental and behavioural particularities are tested through an evolutionary approach.

The model needed to contain agents with specific states and behaviours, as well as some way to designate spaces and resources. Our goal was not to re-create the exact landscape in which Neanderthals lived or to reconstruct their behaviour. Given the few archaeological remains and the general lack of information about their culture, any attempt to replicate Neanderthal behaviour would have to make too many assumptions, and the whole model would be too fragile. Therefore, our idea was to create a simple, abstract model, in which only the traits, behaviours and landscape features that we are interested in are present. On the other hand, because we want to simulate natural selection and a changing landscape in a direct way, we needed a high degree of heterogeneity in the system. For this reason we decided to use agent-based models (ABMs) to explore the issue. This also allowed us to explicitly position single groups of Neanderthals in this heterogeneous environment, as our hypothesis focuses on the relationship between resource distribution and cannibalistic behaviour. Moreover, ABMs allow spatial information to be combined with the agent decision-making process, which was modelled after an evolutionary game theory framework. Finally, high-performance computing was needed to explore the parameter space created by the variables defined in the model.

2. Methods

The first step in our virtual experiment was to define a basic agent-based model. This model was designed to explore the initial situation in which Neanderthals did not have serious competition in their quest for resources. This initial situation defined the environment in which these agents live, as well as the variables and behaviours that characterize them.

The method we propose is a modification of the work done by Epstein and Axtell with Sugarscape, and the research done using simulation in archaeological research, particularly the Artificial Anasazi project, developed at the Santa Fe Institute (Epstein and Axtell, 1996; Diamond, 2002). Studies conducted after that project, published in JASSS, are quite interesting in that they explore the possible pitfalls and problems of the method regarding the simulation of realistic scenarios (Janssen, 2009). Given the hypothesis we want to explore, we do not need to reconstruct the terrain and landscape in which Neanderthals lived with a high level of detail. We need only reproduce the general situation, and for this reason we created general environments able to reproduce situations in which resources are extremely scarce and clustered. The environment is defined as a lattice of variable dimension that in turn defines a field of resources, in keeping with the classic Sugarscape model proposed by Axel and Epstein. Each location has two different values: the current level of resources, and the maximum level of resources that it can produce. At each time step the simulation checks, for each location, whether resources have reached maximum levels. If this is not the case, the current level of resources will have the chance to grow. We created different environments in accordance with these initial characteristics. Fig. 1 shows a basic field of resources, with randomized maximum values in each location. Fig. 2 shows a more realistic landscape. We generated a fractal resource distribution using GRASS GIS (2011), where resources are spatially clustered around rich locations. This solution provides us with an infinite number of environments at the same time. All the environments are different, but at the same time all of them satisfy the requirements.

We defined the basic agent of our system as a group of individuals that form a community. This agent is the atomic decision-making unit of the model. This is because we are interested in decisions focused on resource gathering, which can be abstracted at a group level. The most important state variable of our model is the location of the group. This position, coupled with a defined home range (where the group will collect resources), establishes the area in which the group acquires food. The second state variable is population, which is an abstract index of the number of individuals that form the group. Apart from home range, each group is defined by two additional factors: cannibalism (the tendency of a group to make use of this behaviour in order to acquire resources) and the chance of fission (the possibility that a group will split in two).

Once the variables that make up the state and capabilities of each agent were defined, we then defined the agent's behaviour. As we wanted to keep the model simple in order to explore cannibalistic strategies, the agents did not have any kind of memory, and were not capable of complex decision-making processes. At each time step the groups looked inside their home range from their current location for the best possible new location, with more available resources. After moving into this new position, the group collected resources in each location within the home range. It is important to note that a group seldom exhausted the resources available at a location, as it collected resources in keeping with normal distribution in order to avoid unrealistic greedy behaviour. Finally, population size (based on the number of collected resources) and the chance of fission were determined for the next time step. This last behaviour is a function that takes into account the current population and the chance of fission, as larger groups or groups with a higher chance of fission will have a higher probability of splitting.

The model we have chosen to explore cannibalism with is quite straightforward: when a group does not collect enough resources to maintain its population on a given turn, it attacks groups inside the home range of its current location with a chance equal to its own cannibalistic trait. Every group has a different value for cannibalism, which is fixed during the entire lifetime. The chance depends on this value. If the group uses cannibalistic behaviour following this test, it will attack each group in its home range and, for each of them, consume a number of individuals defined by normal distribution. Finally, food is collected from cannibalism and the population adjusted. A drawback to the design of this mechanism is that each individual generates resources equal to a randomized value in the range used in the locations of the environment.

3. Results

The first steps of the simulation focused on exploring the possible parameter spaces of the different variables. We were particularly interested in the effect of different starting values for the number of groups, the chance of fission and the home range, as well as varied environments. For the first of these, we assumed that the number of groups was not relevant if the chance of fission allowed the groups to populate the entire environment, thus stabilizing the population near the carrying capacity of the system. Different home ranges were tested, and although they modified the carrying capacity of the environment, the final results regarding behaviour were not dependent on this particular trait.