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Ecocultural range-expansion scenarios for the replacement or assimilation of Neanderthals by modern humans

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ABSTRACT

Recent archaeological records no longer support a simple dichotomous characterization of the cultures/behaviors of Neanderthals and modern humans, but indicate much cultural/behavioral variability over time and space. Thus, in modeling the replacement or assimilation of Neanderthals by modern humans, it is of interest to consider cultural dynamics and its relation to demographic change. The ecocultural framework for the competition between hominid species allows their carrying capacities to depend on some measure of the levels of culture they possess. In the present study both population densities and the densities of skilled individuals in Neanderthals and modern humans are spatially distributed and subject to change by spatial diffusion, ecological competition, and cultural transmission within each species. We analyze the resulting range expansions in terms of the demographic, ecological and cultural parameters that determine how the carrying capacities relate to the local densities of skilled individuals in each species. Of special interest is the case of cognitive and intrinsic-demographic equivalence of the two species. The range expansion dynamics may consist of multiple wave fronts of different speeds, each of which originates from a traveling wave solution. Properties of these traveling wave solutions are mathematically derived. Depending on the parameters, these traveling waves can result in replacement of Neanderthals by modern humans, or assimilation of the former by the latter. In both the replacement and assimilation scenarios, the first wave of intrusive modern humans is characterized by a low population density and a low density of skilled individuals, with implications for archaeological visibility. The first invasion is due to weak interspecific competition. A second wave of invasion may be induced by cultural differences between moderns and Neanderthals. Spatially and temporally extended coexistence of the two species, which would have facilitated the transfer of genes from Neanderthal into modern humans and vice versa, is observed in the traveling waves, except when niche overlap between the two species is extremely high. Archaeological findings on the spatial and temporal distributions of the Initial Upper Palaeolithic and the Early Upper Palaeolithic and of the coexistence of Neanderthals and modern humans are discussed.

1. Introduction

Recent archaeological and anthropological findings and analyses suggest that modern humans had reoccupied the Middle East by 55 kya (Hershkovitz et al., 2015) and indicate that they subsequently overlapped with Neanderthals in Europe between about 45 and 40 kya, after which the latter disappeared from Europe (Mellars, 2006a; Benazzi et al., 2011, 2015; Higham et al., 2014; Hublin, 2015; Roebroeks and Soressi, 2016). Although Neanderthal effective population size shows an overall decreasing trend after about 0.5 to 1.0 Mya (Prüfer et al., 2014), the Neanderthal population in Europe during the Middle Palaeolithic may have fluctuated in response to climatic cycles (Hublin and Roebroeks, 2009). Importantly, Neanderthal population appears to have repeatedly recovered when environmental conditions improved and, in particular, may have attained its maximum size, at least in Germany, just before the arrival of modern humans (Richter, 2016). Hence, Neanderthal extinction cannot readily be explained by climate

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change per se, and given that the two species overlapped and likely exploited similar niches (Banks et al., 2008; Hoffecker, 2009; Nigst et al., 2014; Roebroeks and Soressi, 2016), the most plausible cause of the replacement of the indigenous Neanderthals by the intrusive modern humans is interspecific competition.

What competitive advantage did the modern humans have over the Neanderthals (and other archaic human species in Eurasia)? The prevailing view among archaeologists is that modern humans were culturally/technologically more advanced than the coeval Neanderthals, perhaps because they possessed more advanced cognitive abilities (e.g., Mellars, 2006a, b, c; Klein, 2008; Bar-Yosef, 2013; Wynn et al., 2016). However, this interpretation has been contested by Zilhão et al. (2010), Villa and Roebroeks (2014), and Roebroeks and Soressi (2016) who do not see "*substantial* cognitive and technological differences" [italics added] in the archaeological record. These latter authors favor a strictly demographic scenario, whereby the resident Neanderthals were overwhelmed by the numerically superior modern humans. Genetic and archaeological studies do, on balance, suggest that modern humans were more numerous than the Neanderthals (Atkinson et al., 2009; Prüfer et al., 2014; Mellars and French, 2011; Villa and Roebroeks, 2014; Kuhlwilm et al., 2016), but do not provide a compelling explanation for the numerical disparity.

Dependence of the culture/technology level of a human population on its size – a larger population is predicted to have a higher "culture level" – has been the focus of many theoretical (Shennan, 2001; Henrich, 2004; Strimling et al., 2009; Mesoudi, 2011; Lehmann et al., 2011; Aoki et al., 2011; Kobayashi and Aoki, 2012; Fogarty et al., 2015, in press), psychological (Caldwell and Millen, 2010; Derex et al., 2013; Muthukrishna et al., 2014), archaeological (Clark, 2011; Klein and Steele, 2013), and ethnological (Collard et al., 2016; Read, 2006; Kline and Boyd, 2010) studies. These studies treat population size as a *parameter*, determined by undefined causes or manipulated by the experimenter. But culture level may have a reciprocal effect on population size, in which case the latter should also be assumed to be a variable. Moreover, "[a]ny process of population replacement and extinction reduces ultimately to a question of numbers" (Mellars and French, 2011).

Mathematical models of the coupled dynamics of the size and culture level of a population, where both quantities are variables, are therefore more relevant (Lee, 1986; Ghirlanda and Enquist, 2007; Richerson et al., 2009; Aoki, 2015). They show that the population (in isolation) may exist in either of two states: large with a high culture level, or small with a low culture level. Historical contingency may then determine which of these equilibria is reached. Importantly, the empirical observation that population size and number of tool types are not correlated in ethnographic hunter–gatherers (Collard et al., 2016) does not invalidate these models – the sampled populations may be distributed around just one of the two equilibria – as argued by Aoki (2015).

A standard model of interspecific competition is the Lotka–Volterra (LV) model (Shigesada and Kawasaki, 1997), which tracks size changes in two competing populations. Gilpin et al. (2016) introduced into this framework an interaction between the size and culture level of each of two competing *regional* populations, the Neanderthals and modern humans. Specifically, innovations that raise culture level were assumed more likely to occur in larger populations, and the carrying capacity of each species was assumed to be a function of its culture level. The dynamics of each species in isolation allow bistability as noted above. When both species are considered together, the interaction between population size and culture level produces multiple equilibria, but most importantly allows a population with a higher culture level but a smaller size to outcompete a larger population at a lower culture level.

Spatially explicit mathematical and/or computational models of the invasion by modern humans and their eventual replacement of resident Neanderthals have taken several different forms. In an early model (Flores, 1998), competition of the LV type, with a viability advantage assumed for modern humans, was extended to include diffusion (random non-directional migration) by modern humans (but not the Neanderthals). A sequel model (Flores, 2011) – and a subsequent closely related one (Wang and Lai, 2012) – allowed diffusion by both competing species and gave rise to traveling wave solutions of the type known for the Fisher–KPP equation (Fisher, 1937; Kolmogoroff et al., 1937). In a different vein, Aoki (1998) formulated a reaction–diffusion model assuming culture/technology transfer from modern humans to Neanderthals, which predicted that the Middle Palaeolithic would be replaced by transitional cultures (e.g., Châtelperronian), which in turn would be replaced by the Upper Palaeolithic (Welker et al., 2016).

A spatially explicit computational model for the spread of modern humans into regions occupied by Neanderthals was proposed by Currat and Excoffier (2004, 2011) and Currat et al. (2008). Their model assumes a demographic advantage to modern humans that entails eventual replacement and shows that even a small amount of interbreeding at the wave front would result in massive introgression of Neanderthal genes into modern humans, which is contrary to observation (Green et al., 2010; Reich et al., 2010; Prüfer et al., 2014). They conclude, therefore, that there were obstacles to interbreeding.

The spread of Neolithic farmers across Europe was one of the first archaeological applications of the Fisher–KPP wave of advance model (Ammerman and Cavalli-Sforza, 1971, 1973, 1984), yielding a theoretical prediction for the speed of expansion consistent with the empirical estimate of about 1 km/yr. More complex reaction–diffusion models allowing for conversion of indigenous hunter–gatherers to farming have also been proposed (Aoki et al., 1996).

A modified Fisher–KPP model incorporating a time delay between successive migrations (equivalent to the mean generation time) was subsequently applied to the post-LGM recolonization of Europe by Upper Palaeolithic hunter–gatherers (Fort et al., 2004), where the speed inferred from archaeological data is 0.4–1.1 km/yr. Based on a limited amount of data (Bar-Yosef and Pilbeam, 2000; Stringer et al., 2000; Fort et al., 2004) suggested that the speed of the modern human wave of advance into the Levant and Europe was 0.5 km/yr. With a larger data set of calibrated radiocarbon dates, Mellars (2006a) produced an estimate of perhaps 0.4 km/yr for the rate of spread of modern humans from the Levant into Europe. The latter two estimates pertain to the case where modern humans were invading regions occupied by Neanderthals, as opposed to the former where spread was likely into empty space. Interestingly, the latter two estimates (0.5 km/yr and 0.4 km/yr) are at the lower end of the range of the former (0.4–1.1 km/yr), which is consistent with the theoretical predictions of the diffusive LV competition model (Shigesada and Kawasaki, 1997).

Reaction–diffusion models have also been applied to competition between exploiters and altruists (Wakano, 2006) and to competition between individual and social learners (Wakano et al., 2011).

In the present study we investigate theoretically the spatial spread of modern humans into regions, including non-European Eurasia, occupied by Neanderthals and/or other archaics. Our goals are to obtain the conditions under which the former can replace or assimilate the latter, to predict the speed at which replacement or assimilation will occur given that it does, and to estimate the duration of regional overlap (coexistence) of the two species. To do so, we formulate a reaction–diffusion model that introduces, into our previous model (Gilpin et al., 2016), spatial structure and diffusion between neighboring regions of this space. Our ecocultural model differs from the standard diffusive LV competition model in that the carrying capacities of the competing species are not arbitrarily