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Was inter-population connectivity of Neanderthals and modern humans the driver of the Upper Paleolithic transition rather than its product?

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A B S T R A C T

The transition from the Middle Paleolithic (MP) to the Upper Paleolithic (UP), circa 40kya, is viewed as a major turning point in human evolution, in terms of the material culture, demography, and geographical expansion of modern humans. However, attempts to identify an origin of this so-called ‘revolution’ in the form of a particular stone-tool techno-complex, representing cultural modernity, which spread across the human range, have failed. Instead, the archaeological record of this period comprises multiple ‘transitional techno-complexes’, some associated with modern humans and others with Neanderthals. The cultures that these techno-complexes represent are characterized by precursors of the material cultures of the UP, often alongside features that suggest local cultural continuity. The broadly simultaneous appearance of these transitional cultures, despite a lack of a clear common origin, is puzzling. We suggest that these local ‘revolutions’ had a common underlying driver, which explains the simultaneous appearance of transitional techno-complexes, but that this driver did not determine the particular form of each local revolution. We propose that the driver of the transition to the UP was an increase in inter-population connectivity, both within- and between-species, which allowed local cultures to rapidly evolve and to attain greater complexity than ever before. We suggest that this change was driven by the interaction between modern humans and Neanderthals. In this article we outline processes that are likely to have influenced inter-population connectivity, bringing together evolutionary and ecological perspectives alongside insights from the field of cultural evolution.

1. Background: shattered expectations, and a suspicious coincidence

1.1. The prominent view until recently and its shortcomings

Until recently, the most prominent view of the Middle Paleolithic (MP) to Upper Paleolithic (UP) transition portrayed it as a revolution rather than an evolution of local cultures. This revolution was regarded as the result of an out-of-Africa migration, driven by a cultural or cognitive change that provided its carriers with an advantage over local populations (e.g., Eswaran et al., 2002; Henshilwood and Marean, 2003; Klein, 2008, 2003; Smith et al., 2005; Stringer, 2003). According to recent versions of this account, the migrants, modern humans (henceforth *Moderns*), interbred to some extent with the local hominin populations they encountered — Neanderthals, Denisovans, and possibly others — and rapidly replaced them as they spread throughout Eurasia (d’Errico and Stringer, 2011).

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One prediction from such an account is that the archaeological record should reflect the migrants' material culture. Accordingly, during the period of 40–50kya we should expect to observe an archaeological horizon characterized by a techno-complex that is shared across archaeological sites. This prediction is not borne out. The first culture that is clearly UP in its characteristics and that is arguably shared across relatively many sites in different regions is the Proto-Aurignacian (Benazzi et al., 2015; Mellars, 2006; Stutz, 2015). In most sites it is found late within the expected time frame (42-35kya), and is often preceded by material cultures that differ between sites and regions, as well as from the MP cultures that had characterized Eurasia previously for tens of thousands of years. In other regions, such as in Western Europe, the Proto-Aurignacian culture is found contemporaneously with such cultures (Teyssandier, 2008; Tsanova, 2013, 2012). Another material culture that has been suggested as a marker of the spread of Moderns is the Aurignacian itself, dated in most places to 40-30kya (see Nigst et al., 2014). It also does not meet the prediction: it is preceded nearly everywhere by early UP cultures, not by MP ones. Moreover, the Aurignacian is found in the Levant significantly later than its first appearance in Europe, suggesting that it did not spread from the Levant into Europe, but rather in the opposite direction (Bar-Yosef and Belfer-Cohen, 2004; Goring-Morris and Belfer-Cohen, 2006).

A second prediction following this view of the MP-UP transition is that if there were such an 'invading' culture, it would presumably be found first in Africa, and would have spread later to the Levant, and thence to Europe. No such pattern is to be found: Neither the Proto-Aurignacian nor the Aurignacian emerge from Africa (e.g., Conard, 2008). Technologies found in the Levant share close affinities with the Proto-Aurignacian, and may partially fit the bill, if interpreted as originating among Moderns in the Levant and spreading with them from there. However, although the Moderns' spread throughout much of Eurasia took place around 40kya (see, e.g., Higham et al., 2014; Hublin, 2012; Mellars, 2004; Nigst et al., 2014), Moderns first occur in the Near East and particularly in the Levant tens of thousands of years earlier (Groucutt et al., 2018; Hershkovitz et al., 2018; Mercier et al., 1993). Accordingly, the cultural dynamics there may have been different from those in the rest of Eurasia,[1] as will be discussed below.

Finally, the main tenet of the 'revolution account' of the MP-UP transition is that one population, along with its culture, replaced the other. This is not supported by most current interpretations of the archaeological record (d'Errico and Stringer, 2011; Hovers and Belfer-Cohen, 2006; Straus, 2005; Teyssandier, 2008; Tsanova, 2013). Rather, it seems that cultural dynamics reflected in the archaeological record near the MP-UP transition are often better characterized as cases of local cultural evolution (Barton and Riel-Salvatore, 2012; Hovers, 2009a; Kuhn, 2013; Stutz, 2015; Stutz et al., 2015).

1.2. The MP-UP transition: multiple transitional assemblages

The end of the MP, approximately 50–40kya, is marked by the appearance of multiple so-called *Initial Upper Paleolithic* (*IUP*) *techno-complexes*, a term partially overlapping the term *transitional techno-complexes*, or *transitional assemblages* (*TAs*).[2] In most cases, authorship of these assemblages is unknown or debated, and some could potentially have been authored by both Moderns and Neanderthals (Bosch et al., 2015; Douka et al., 2014, 2013; Gilead, 1991; Higham et al., 2010; Hoffecker, 2009; Hublin, 2015; Richter et al., 2008; Škrdla, 2017; Stutz, 2015; Tostevin, 2012, 2007; Tostevin and Škrdla, 2006; Zilhão et al., 2006; Zwyns et al., 2012). These assemblages are characterized by their combinations of MP technology – such as the Levallois industry – and characteristics associated with the UP such as new methods of blade production (Barzilai and Gubenko, 2018; Hublin, 2015; Kuhn et al., 2009; Marks, 1983).[3] Some of these assemblages reflect regional cultural continuity with respect to various aspects of the tool production, while others seem geographically intrusive. In many cases, the details of the 'advanced' features are not shared across TAs. They can be viewed as evidence of cultures that are different, and at times of higher technological complexity, than those of the MP, but not necessarily with a common origin.

1.3. An (unconvincing) alternative account of the MP-UP transition

An alternative account for the MP-UP transition and the emergence of the TAs, which might be called the *independent local evolution account*, proposes that each of the TAs emerged as an endemic local modification of the MP culture that existed locally and that preceded it (d'Errico, 2003; Faivre et al., 2017; Slimak, 2008; Zilhão and d'Errico, 1999). This would explain the local continuity seen in many TAs with respect to the preceding MP culture. Notably, it seems that the majority of TAs appeared rather abruptly on an archaeological time scale (with the exception of the fairly gradual emergence of TAs in the Levant; e.g. Belfer-Cohen and Goring-Morris, 2007).

However, the independent local evolution account yields a crucial prediction that is not realized: if the different local evolutionary dynamics that led to the cultural transitions were independent, the timing of each TA emerging from a MP substrate that had existed for tens of thousands of years should be independent of the others. Accordingly, their emergence would then be distributed in time throughout the MP. This is not the case. Instead, TAs appear clustered in time, emerging mostly 50–40 kya. This correlation in timing constitutes a *suspicious coincidence* and begs the question: why did seemingly independent events appear in such a coordinated manner?

2. A path forward: searching for a *non-determining driver* of cultural change

We propose the *Common Non-determining Driver Hypothesis*: we suggest that the punctuation events that gave rise to the TAs shared a common driver, which determined their occurrence within the particular timeframe of 50–40kya, but did not directly determine the cultural content of each local evolutionary process. Thus, each such process resulted in a unique outcome, giving rise to a diverse assortment of TAs across Eurasia in this period.

What could the non-determining driver have been? A natural candidate is a change in the environment: it is reasonable that a global environmental change could occur, affecting multiple populations at the same time. Although hard to rule out, this

[1] Much of Eurasia outside of Europe and the Levant is not discussed in depth here, due to the sparse archaeological record there from the MP-UP transition.

[2] The distinction between these terms is based on the extent of local continuity compared to novel elements or elements from elsewhere, and is debated. We use the abbreviation *TA* (Transitional Assemblage) throughout the manuscript for simplicity, invoking 'transitional' in the context of transition between MP and UP, not necessarily asserting local continuity or otherwise with respect to each assemblage. We use this term fairly loosely to represent cultures that are relevant to the discussion at hand and that combine both MP and UP characteristics.

[3] In this study we refer primarily to the lithics, which are best preserved in the archaeological record. We treat these as a proxy for the cultures they represent, and their complexity, although this assumption is debatable. This is discussed briefly below.

explanation is debated and in itself seems unlikely to provide a sufficient explanation for the contemporaneity of the TAs. First, the magnitude of environmental changes during the period of 50–40kya was not greater than fluctuations that had occurred during the MP and which did not trigger significant cultural change (Davies et al., 2015; Petit et al., 1999; Van Andel and Tzedakis, 1996; Willerslev et al., 2014; but see Finlayson, 2004; Finlayson and Carrion, 2007; Müller et al., 2011 and the discussion in Robert and Richter, 2018). In many regions there is also no dramatic change in the fauna and flora reconstructed from remains in hominin occupation sites (accumulated both naturally and anthropogenically; e.g. Belmaker and Hovers, 2011; Shea, 2003; Stiner and Bar-Yosef, 2005; Stiner and Tchernov, 1998; but see the challenges of resolving contradictory findings in Finlayson and Carrion, 2007). Second, any global environmental change is expected to influence populations in different environments quite differently, for example by rendering some regions less hospitable to hominin species and others more hospitable to them (d'Errico and Goñi, 2003; Finlayson, 2004; Rohling et al., 2013). It is unlikely that such different influences would lead to the qualitatively similar trend seen in the various TAs in populations across a range of environments. This is not to say that climate did not play a role in the MP-UP transition; for example, the different regional expressions of global climate change could have triggered cascading effects with far-reaching implications. Climatic influence and its possible interaction with other factors are discussed below.

In what follows, we propose in section 3 the *population inter-connectivity theory*, which considers insights from models of cultural evolution in suggesting that the non-determining driver may have been an increase in the rate or extent in which different populations interacted. In section 4 we briefly summarize relevant findings from the archaeological record of the MP-UP transition. Section 5 elaborates on some model-derived underpinnings of our suggestion, and offers a brief portrayal of the demographic and cultural dynamics in the Levant and Near East of Moderns and Neanderthals, and their interactions. Our theory is laid out in detail in section 6, which, rooted in a range of scientific disciplines, outlines multiple processes that may have influenced inter-population connectivity. Section 7 provides a brief summary, draws some conclusions, and highlights avenues for future study.

As a first step to learning about the possible nature of the common non-determining driver of the emergence of TAs, we suggest exploring possible parameters that could influence cultural evolution.

3. Hypothesis: the population inter-connectivity theory

3.1. The parameters of cultural evolution

A significant body of literature, accumulated over recent decades, is devoted to modeling the dynamics of cultural evolution. One of the focal questions in this field is *What are the determinants of cultural complexity*. Across multiple models with quite different assumptions (e.g., Aoki, 2018; Henrich, 2004; Henrich et al., 2016; Kolodny et al., 2015a; Lehmann et al., 2011; Mesoudi, 2011; Powell et al., 2009), the size of the population in which the culture evolves emerges as one of the most prominent parameters of the cultural evolutionary process, and one that strongly determines cultural complexity.[4]

However, there was no known climatic or environmental shift at 50-40kya that is likely to have triggered sudden broad-scale population growth (Davies et al., 2015; Finlayson and Carrion, 2007; Lowe et al., 2012; Morin, 2008; Petit et al., 1999; Van Andel and Tzedakis, 1996; Willerslev et al., 2014); also, there is no evidence for an increase in population size in this period across the geographic range in which TAs are found. Rather, such an increase seems to have begun well after the transition to the UP (Bocquet-Appel et al., 2005; Bocquet-Appel and Degioanni, 2013; Mellars et al., 2011).[5] Therefore, population growth *in itself* is not likely to have been an external driver of local emergence of complex TAs at multiple localities.

On the other hand, several models of cultural evolution propose that the parameter of importance may not be the population size per se, but a related concept, fashioned after the concept of *effective population size* in population genetics, and dubbed, accordingly, the *effective cultural population size* (ECPS) (Creanza et al., 2017; Kolodny et al., 2015a; Premo, 2015; Shennan, 2001). The ECPS is dependent on the actual number of individuals in the population, but also on other factors. Importantly, it is affected by the way the population is sub-structured. For example, cultural knowledge may not be shared by the whole society, but be concentrated in a subgroup, such as medicine people, religious leaders, or specialists in certain tool manufacture and usage (Kolodny et al., 2015a). Alternatively, the population could be composed of several sub-populations that regularly exchange migrants, in which case the ECPS is dramatically increased with increasing connectivity between populations (Creanza et al., 2017; Derex et al., 2018; Derex and Boyd, 2016; see Box 1). Thus, ECPS can increase significantly even without any change in the number of individuals.

3.2. Population inter-connectivity

Based on these ideas, we propose the *population inter-connectivity theory*: namely that an increase in inter-population connectivity across Eurasia, and particularly an increase in interactions between culturally divergent populations, was the main driver of the coordinated local processes of cultural evolution, which gave rise to locally-evolved TAs in the MP-UP transition. We suggest that the increase in connectivity could have occurred via a combination of long-distance population dispersals and an increase in intensity of local networks of inter-population interaction, both within each species, Moderns and Neanderthals, and between them.[6] A number of researchers have proposed ideas related to this hypothesis, namely that many of

[4] We follow these studies and others in using a loose definition for cultural complexity, which encompasses either or both of (1) the size of a population's tool repertoire, and (2) the inclusion in the repertoire of tools whose structure or manufacturing combine multiple elements, materials or techniques.

[5] The question of regional population densities and how they are related to population growth on a long-historical timeline (*long durée*) is far from resolved; in the Levant particularly, opposing assertions have been made (e.g., Hovers, 2009b, 2006; Speth and Clark, 2006; Speth, 2013; Speth and Tchernov, 2002; Stiner et al., 2000, 1999). However, population growth that is not driven by cultural change but that drives it is likely to occur primarily due to climatic factors, which, as discussed earlier, would have had varied influences on regions across the range of hominin habitation. Environmental change that would spur *coordinated* population increase across the Levant and Europe, and would encompass the range in which TAs are found, seems unlikely. We therefore regard environmental changes alone to be insufficient to *independently* explain the UP transition, but they may have interacted with other factors to bring about the transition, as discussed below.

[6] Whether Moderns and Neanderthals should be considered distinct species or subspecies is unimportant as long as the nature of the genetic relationships between the two groups and the meaning attached to the chosen labeling is clear. We remain agnostic regarding the optimal choice of terminology, and for simplicity address the two meta-populations as separate species, using the term introgression to describe the sharing of genetic material between them.

the TAs are products of local evolutionary processes, which are influenced by interaction with intrusive cultures, usually attributed to Moderns (Conard, 2010, 2008; Hovers, 1998; Hublin, 2012; Kuhn and Zwyns, 2014; Stutz, 2015; Stutz et al., 2015). Our proposal adds to these ideas a unifying framework that links the suspicious coordination in the timing of the emergence of the TAs with an eco-evolutionary perspective and insights from models of cultural evolution.

3.3. *Prominent considerations and postulates for the current discussion*

It is reasonable to assume that Moderns and Neanderthals were culturally divergent when they met in the Levant and perhaps also during later interactions. However, it is important that cultural divergence need not have remained correlated with genetic divergence (Hovers, 2009b, 2006). We posit that groups of the two species admixed during this period and before it, perhaps as early as 120kya, genetically and culturally, to various extents (Bar-Yosef and Bordes, 2010; Hajdinjak et al., 2018; Kuhlwilm et al., 2016; Sankararaman et al., 2014; Tostevin, 2007; Villanea and Schraiber, 2019). Thus, in what follows, where we discuss Modern-Neanderthal cultural interactions we refer to cultural increase in interactions between divergent groups. Except where specified otherwise, we posit that the discussed dynamics were true for divergent groups both within and between species, divergence that emerged as a result − for example − of long-standing geographical substructure of the meta-population (Gunz et al., 2009; Hajdinjak et al., 2018; Prüfer et al., 2014; Wall et al., 2013; Yang et al., 2017).

In this study we consider a range of types of possible ecological and cultural interactions, which span different temporal and spatial scales. We discuss predictions with respect to the broad conditions in which these interactions occur, and suggest that they overlap in their qualitative influence on culture. These interactions include, for example, contact between neighboring groups that observe one another from a distance or only briefly, in hostile or friendly manners; such interactions may also arise following short- or long-distance migration of groups. At the other extreme, interactions may include cases in which individuals from one group are accepted into another (or forced to join), representing frequent exchanges between neighboring groups or rare events associated with long-distance dispersal. These different types of interactions may facilitate various social learning dynamics, ranging from those associated with social intimacy, which would allow transmission of detailed culturally-determined techniques, to transmission of cultural information via stimulus diffusion, which would not include full transmission of the detailed procedures associated with it (see, e.g., Tostevin, 2007). Such information could, for example, include the idea of a certain behavior or type of tool that can be produced. The time scale of cultural interactions that we consider is on the order of thousands of years; long enough even for groups that generally interact only rarely and superficially to exchange some individuals, allowing for detailed transmission of techniques and practices.

It has recently been shown that cultural complexity can be profoundly influenced by interactions between culturally divergent populations. Under certain parameter regimes, even a slight increase in rates of interaction can drive dramatic cultural 'explosions' (Creanza et al., 2017). In that study, a very simple model of the interaction between two cultures suggests that when different cultural groups meet, their interaction may give rise to a new culture with complexity far greater than the mere sum of the "parent" cultures. In addition to elements of the two cultures, the emergent culture could include new cultural traits that emerge via combination and recombination of the "parent" cultural elements and through generalizations that their joint occurrence may facilitate (Creanza et al., 2017).

Box 1
Inter-population interactions

> For the dynamics of inter-population connectivity, it is useful to consider explicitly when and how interactions between populations could take place.
>
> Inter-population contact, both within and between the two species (Neanderthals and Moderns), may occur in a number of ways: (1) via translocation of individuals from one hunter-gatherer band to another, willfully or by force; (2) via trade interactions between representatives of the bands, occurring near residential sites or at open air temporary localities; (3) via meta-population dynamics, or fission-fusion dynamics, in which band composition changes frequently with individuals moving between bands (Hill et al., 2014, 2011).
>
> For the dynamics discussed in this study, each of these factors may have played similar qualitative roles. However, considering each of these dynamics explicitly in future work may be productive, as they may differ in the predictions to which they give rise. For example, they may differ with respect to the rapidity and directionality in which genetic admixture could have occurred, whether the effect of contact during the interaction was symmetric, or which type of evidence is most likely to have been left behind and might allow us to learn about these interactions.

Such combinatorial and generalization processes of cultural innovation can give rise to a vast number of possible new traits. Therefore, a culture that arises in this manner from the interaction between two culturally-divergent groups would necessarily incorporate only a small sample of the many possible complex traits that could arise from the interaction of the two populations' cultural repertoires. Thus, when a group from one culture interacts with a group from another culture, the emerging outcomes are likely to differ every time (Creanza et al., 2017). Accordingly, we should expect that in each specific locality where culturally divergent Neanderthals and Moderns interacted, the emergent culture would differ from cultures that arise following similar interactions elsewhere.

In what follows, we first discuss briefly some observations regarding the TAs and the links between them, and then discuss in more detail the effect of inter-population interactions on culture. We then outline a number of scenarios for processes that may have led to increases in inter-population connectivity, both within and between the two groups, Moderns and Neanderthals, in a way that could have played a role in driving the coordinated emergence of the TAs. These scenarios are grounded in what is known about Neanderthal-Modern interactions and population dynamics near the MP-UP transition. They are not mutually exclusive, and the different processes that they include may have resulted from, or been driven by, local changes in demography or climate that have been the focus of many previous studies.

4. The archaeological record 50–40 kya

Three major questions are usually addressed with respect to the assemblages that span the MP-UP transition: their timing, whether they should be attributed to Moderns or to Neanderthals, and how they relate to other known assemblages. Even a superficial review of the archaeological record from this period is far beyond the scope of this section; instead, we present a brief summary and suggest a synthetic view of the findings.

The earliest TA, and perhaps the most classical one, is the Initial Upper Paleolithic (IUP) appearing in the Levant, sometimes referred to as the Emiran (Bar-Yosef and Belfer-Cohen, 2010; Barzilai and Gubenko, 2018; Boëda et al., 2015; Bosch et al., 2015; Kuhn, 2003; Kuhn et al., 2009; Marks, 1983; Meignen, 2012). It seems to have evolved gradually and locally, incorporating prominent elements of the Levantine Mousterian, and sharing 'advanced' elements with the Early Upper Paleolithic Ahmarian that follows it in this region. The Emiran shares very close affinities with East and Central European assemblages, the Bachokirian and Bohunician. These assemblages in Europe appear to be intrusive, with little or no resemblance to the local MP cultures that preceded them, suggesting that the Emiran may have originated in the Levant and spread from there (Hoffecker, 2009; Mellars, 2006; Richter et al., 2008; Škrdla, 2017, 2003, Tostevin, 2000, 2012).

In contrast to these intrusive TAs, multiple TAs in West and Central Europe display a local MP tradition with variable proportions of newly emerged UP features. These TAs, such as the Szeletian, the Lincombian-Ranisian-Jerzmanowician (LRJ), the Châtelperronian and the Uluzzian, are typically interpreted as a local evolution from the late MP groups that incorporated new technologies (Flas, 2011; Hublin, 2015; Mussi, 2002; Nigst, 2012; Ruebens, 2013). Hominin remains have been found in clear association only with the Ulluzian (Modern), the Châtelperronian (Neanderthal), and the LRJ (Neanderthal) (Hajdinjak et al., 2018; Semal et al., 2009) but these associations have been questioned (Banks et al., 2013; Bar-Yosef and Bordes, 2010; Higham et al., 2010; Zilhão et al., 2015).

The emerging picture of Eurasia between 50 and 40kya is of a complex technological landscape, consisting of many contemporaneous cultural traditions, sometimes in relatively close geographic proximity to one another. During this period, groups of Moderns and Neanderthals interacted extensively across the continent, interbreeding repeatedly (Kuhlwilm et al., 2016; Racimo et al., 2015; Sankararaman et al., 2016; Slon et al., 2018; Vernot et al., 2016; Yang et al., 2017), exchanging pathogens and parasites (Chen et al., 2017; Enard and Petrov, 2018; Pimenoff et al., 2016), with Moderns eventually replacing Neanderthals. Given the evidence of close contact between the species, it is likely that extensive cultural interactions also took place among different groups within and between the two species, and that the diversity of the lithic assemblages reflects these interactions.

Therefore, attempts to dichotomously associate each assemblage with a particular species should be avoided in favor of the search for relations between assemblages from a cultural evolutionary perspective.[7] Each assemblage, and each particular instance of it at a certain site, may constitute a snapshot of a dynamically changing technology. This is not to say that categorization is unimportant, but that a focus on evolutionary questions such as differentiation between homology and analogy of shared technological features found in different assemblages, considering possible multi-way cultural interactions, may be constructive (Kuhn, 2003).

5. Population inter-connectivity: models of cultural evolution, and the specific geo-demographic context

5.1. Not all inter-population interactions were made equal

Connectivity between populations can drive cultural change via direct spread of ideas. However, it can also increase cultural complexity (as defined above), as often appears to be the case in the transition between MP techno-complexes and the TAs. This increase could occur in two main ways, which are not independent but whose separate consideration may be useful. One is by increasing the number of interacting individuals in what can be thought of as a common culture. This would be the case if two hunter-gatherer bands of the same ethnicity and meta-culture, whose territories lie a short distance from one another, begin to interact. The resultant increase in cultural complexity that would be seen in each group is driven simply by the increase in the ECPS: every individual would be exposed, directly or indirectly, to a large number of potential innovators and cultural practitioners from whom to learn and whose innovations can spread. Cultural traits may become known to more people and are at a reduced risk of being forgotten (i.e. stochastically lost from the population). Such an increase in cultural complexity can be considered a steady-state phenomenon, and could be maintained as long as interactions continue and the population that is effectively sharing the culture remains connected.

A second way in which cultural complexity can increase via inter-population connectivity is through the interaction of individuals from different cultures. Intuitively, cross-cultural interactions are likely to give rise to innovation. To consider this effect systematically, an explicit model — even a simple one — is needed. Studies across a number of fields have suggested such models or considered related phenomena (e.g., Anthony, 1990; Boyd and Richerson, 1985; Cavalli-Sforza and Feldman, 1981; Hill et al., 2014; Kobayashi et al., 2016). A common treatment of cross-cultural interactions posits that such interactions produce cultural traits that are combinations of traits from the two original cultures, such as a tool type originating in one culture modified by a method used for tool production in the other; utilization of a tool in a new cultural context; or the incorporation of a practice into a new cultural setting. Besides such combinations of traits, studies of innovation and creativity also ascribe a major role to (conscious or unconscious) drawing analogies from existing knowledge and to placing ideas in new conceptual contexts (d'Errico and Colagè, 2018; Fogarty et al., 2015; Hovers, 2012; Kaufman and Beghetto, 2009; Kolodny et al., 2015a, 2015b; Madjar et al., 2011; Merrotsy, 2013; Youn et al., 2015).

Here, we do not subscribe to a particular model of cultural interaction or cultural innovation; we merely assume that processes similar to those described above take place when cultures meet and their bearers interact (Text box 1). This leads to a rather obvious, yet powerful, observation: the expected extent of cultural innovation resulting from cross-cultural interaction is tightly linked to the degree of cultural difference. An interaction between two cultures that had been developing independently can bring together suites of traits that differ significantly, giving rise to an

[7] The focus on species' authorship of lithic assemblages encourages a false implicit assumption, that each species was a meaningful cultural unit. However, multiple lines of evidence, genetic and archaeological, suggest that both Modern and Neanderthal populations were structured. Thus, different groups of the same species could have had different technologies at any particular time. Each such group would be the meaningful cultural unit to study, with respect to its cultural relations with other groups, regardless of its species' affiliation (see, e.g., Hovers, 2009b).

enormous number of potential new combinations of ideas and traits.[8]

These dynamics of cultural change would be most rapid when the inter-population system is out of equilibrium, i.e. when cultures that had not interacted for a long time suddenly begin to interact. Such an interaction would lead to a punctuated burst of cultural complexity following the interaction's onset. Whether the new complexity would be retained or not, and the system's eventual cultural steady state, depend on the conditions of this process, such as whether the interaction is maintained and whether the population size before and after the interaction remains the same (Creanza et al., 2017; Kolodny et al., 2016).

The distinction suggested here between the two effects of inter-population connectivity is superficial. For intermediate rates of population interaction, cultures that are in contact can remain distinct from one another, and what we described here for clarity as two processes at the extremes – an assumption of complete identity between the two interacting cultures at one extreme and an assumption of a long cultural separation between the cultures at the other extreme – would both have roles in dynamically determining cultural complexity and its inter-population diversity (e.g., Derex et al., 2018; Derex and Boyd, 2016).

5.2. A release from an impasse in the Levant

Groups of Moderns reached the Levant tens of thousands of years prior to their further spread throughout Eurasia (Hershkovitz et al., 2018; Mercier et al., 1993; Vaks et al., 2010, 2007), while Neanderthals seem not to have reached further south. The two species most likely interacted, at least intermittently, in this region over extended periods of time, along a fairly narrow front of interaction (Banks et al., 2008; Hovers, 2006; Kuhlwilm et al., 2016; Rak, 1993; Shea, 2003, 1998; Valladas et al., 1999; Vernot and Akey, 2014; Villanea and Schraiber, 2019). The localization of the interaction front to the Levant for such a long period of time until Moderns eventually began spreading from the Levant into other parts of Eurasia is puzzling, especially in light of the relative rapidity with which this spread eventually occurred: Neanderthals were replaced throughout the rest of Eurasia within a few thousand years, between 45–39 kya (Higham et al., 2014). The possible factors that caused this longstanding impasse and its eventual removal have received relatively little attention (but see, e.g., Hovers, 2006; Rak, 1993; Shea, 2006, 2003). We have recently suggested elsewhere (Greenbaum et al., 2018) that this impasse may have been due to inter-species disease dynamics, which constrained Modern-Neanderthal interactions and their spread into one another's regions, until each species became tolerant to the pathogens that had co-evolved with the other species. Other prominent factors that could have triggered the spread of Moderns beyond the Levant, not mutually exclusive with respect to one another nor to the inter-species disease dynamics that we proposed, are demography, climate, and their interaction. In particular, an appealing yet debatable explanation is that climatic change allowed increased mobility across geographic barriers that previously restricted hominin migration (Langgut et al., 2018) and led to an increase in population size or density in the Levant (or strengthened an existing trend of such an increase; see, for example, the discussions in Speth and Clark, 2006; Speth, 2013; Stiner et al., 2000, 1999). Together, these could have enabled and triggered the spread of Moderns northwards.

Regardless of which factor geographically localized the contact-zone of Moderns and Neanderthals, and which process eventually released the restriction, the sudden spread of Moderns beyond the Levant is highly likely to have been the process that sparked the local cultural revolutions at the interface between the Middle and the Upper Paleolithic.

Thus, we suggest that the most straightforward, and perhaps the major, drivers of each of the local cultural transitions were Neanderthal-Modern cultural interactions. Prior to the renewed contact around 50-40kya, the two species had been largely separated for hundreds of thousands of years, a period that is likely to have allowed substantial cultural divergence. It is reasonable to assume that the two species differed in their languages, behavioral norms, and ways of thought, and possibly also in some of the tools that were composed of degradable organic material and are not represented in the archaeological record (see, e.g., Mathew and Perreault, 2015). Therefore, significant cultural transitions would have occurred when groups of the two species interacted. These transitions would have been different in each region, due to the specific conditions of each encounter (e.g., Hovers, 2009a) and due to the stochasticity of such dynamics, giving rise to different local cultures.

The lithic artifacts left by groups of the two species in the Levant during the MP are largely indistinguishable (e.g., Hovers, 2009b). This may simply be due to the limited lithics-focused perspective that we have on cultural behaviors from this period. Alternatively, it may be related to the particular history of inter-species interaction in the Levant: in this region, the two species may have interacted, albeit in a constrained way, within a region that is limited to an area near the interaction front (Greenbaum et al., 2018), for tens of thousands of years prior to the end of the MP. This could have led to gradual convergence of some components of the two species' cultures in this region.

Thus, it might not be coincidental that in the Levant the transition between the MP and the UP differs qualitatively from the transition in most of Europe. In the Levant we see an increasing degree of variability in the lithic material toward the very end of the MP (Abadi, 2017; Goren-Inbar and Belfer-Cohen, 1998; Hovers, 1998). This may reflect a gradual shift from the 'cultural equilibrium' that seems to characterize the majority of the MP, in the Levant and elsewhere, and may be the product of ongoing between-species cultural interactions, and perhaps also a gradual increase in such interactions over time (Greenbaum et al., 2018; Hovers, 2006, 1998; Hovers and Belfer-Cohen, 2013). It is followed by multiple TA variants in Boker Tachtit, Ksar Akil, Um el Tlel, Tor Sadaf and elsewhere, leading eventually to the Ahmarian (Bourguignon, 1998; Fox and Coinman, 2004; Kuhn, 2003; Kuhn et al., 1999; Ploux and Soriano, 2003; Volkman, 1983; Williams and Bergman, 2010). The Levantine MP-UP transition is the one that begins the earliest and is the most gradual, reflecting clear local continuity, as may perhaps be expected in dynamics of long, intermittent, constrained interaction between two divergent

[8] Incompatibilities between cultural ideas and practices may also hinder the full realization of the potential of such meetings of cultures (Ford and Chan, 2003; Henrich, 2001; Rogers, 2010). However, we suggest that such hindrance is likely to be short lived compared to the time scales of inter-population interactions that we consider, i.e. thousands of years. For comparison, even the strictest of cultural taboos in human societies in historical times failed to prevent some amount of genetic admixture, which was necessarily accompanied by transmission of cultural knowledge (e.g., Bamshad et al., 2001; Shen et al., 2004). Moreover, no single cultural group has remained stable and isolated since the late Bronze Age, suggesting that cultural isolation between neighboring populations for such timescales is unlikely. Even from the conservative perspective that cultural taboos or incompatibilities would limit the realization of the *full scope* of the potential interactions, superficial interactions could allow an increase in cultural complexity far beyond that seen in each of the individual cultures before the interaction. Additionally, the available record is biased: only those instances in which the cultural combination resulted in something new would be clearly identifiable; cases in which inter-population interaction failed to give rise to a novel culture would simply be seen as a continuation of one of the previous cultures or replacement of one by the other.

cultures.

Although the Neanderthal-Modern interactions would have gradually shifted the culture of Levantine Moderns in the Levant prior to the formers' spread into Eurasia, we suggest that the cultural differences between the spreading Moderns and the resident Neanderthals across the rest of Eurasia would have been sufficiently large to have played a prominent role in the subsequent emergence of the TAs across this range. However, our theory of population inter-connectivity as the driver of the MP-UP local transitions does not rely on this assumption; even if the Moderns that spread from the Levant did not dramatically differ culturally from the Levantine Neanderthals, we expect their spread to have triggered the emergence of TAs via direct and indirect dynamics considered below.

6. Drivers of increased inter-population connectivity: demography, behavior, selection, and cultural evolution

6.1. Connectivity-increasing demographic dynamics

The spread of Moderns beyond the Levant would have triggered a number of demographic dynamics that are likely to have influenced connectivity patterns beyond the straightforward interaction between the spreading Moderns and the Neanderthal groups they encountered (see Fig. 1).

Importantly, the dynamics discussed here are relevant for interactions of all combinations of the groups involved: Neanderthal-Neanderthal, Neanderthal-Modern, and Modern-Modern. Although the spread of Moderns and the replacement of Neanderthals occurred rapidly on an archaeological timescale and are often portrayed as a clash of two seemingly unified populations, in reality it would have been a drawn-out process that took place over thousands of years. As far as can be interpreted from the archaeological and genetic records, this complex process involved highly structured populations, and is likely to have included cultural cross-fertilization among groups, as much as competition and replacement. These dynamics would have played out between groups of the same species as much as they did between groups of Moderns and of Neanderthals. Moreover, as the TAs clearly demonstrate, cultures rose and fell dynamically within the period of inter-species interaction in Eurasia. It is misleading to focus only on the interaction of “naïve” Modern and Neanderthal cultures, as they had been before contact (laying aside the likely possibility that they interacted in the Levant for tens of thousands of years previously), because it may be that throughout the time 50-40kya, the cultures of most of the hominin groups in Eurasia had already been significantly influenced by inter-species interactions. In other words, the TAs may more productively be thought of as cultures that existed in times when the complete hominin cultural and demographic landscapes in Eurasia were shifting, in a system far away from equilibrium.

During a period in which one species is spreading at the expense of the other, intense demographic turmoil is expected, leading to increased population movement at multiple scales. For example, groups that were faced with strong competition may have been forced to migrate in search of new territory. Some groups may have become fragmented, with individuals dispersing in all directions, while others may have dispersed as a cohesive group. These dispersing groups and individuals were likely to encounter other groups, interact with them, and perhaps join them, directly increasing cultural connectivity and the ECPS. The dispersing groups and individuals would bring with them their original culture, thus increasing the probability of enhancing cultural complexity. Additional, indirect effects, that increase cultural connectivity could also have been created if, for example, migrants maintained active cultural relationships with kin in groups near their place of origin that were not displaced. The movement of individuals and groups may also have triggered cascading migration effects: a group may migrate to new territory, compete with a local group, forcing it to move as well, and so on. In addition, groups and individuals may have moved long distances in search of new territory, thus bringing into contact subcultures that had barely been in touch with one another for centuries or millennia.

The Moderns' spread and the general demographic turmoil could also have brought about extinction-recolonization dynamics, a process of repeated local extinction events, each followed by recolonization of the resulting empty habitat (Hanski, 1998; Wade and McCauley, 1988). These dynamics would free up territories, facilitating, in turn, the arrival of new groups from other regions, and providing ongoing motivation for groups to attempt to colonize vacated territories (i.e. when there's a high chance of finding a new territory that was recently vacated, frequent dispersal behavior, either opportunistic or emerging as a standing cultural trait, is expected to become more common). This, in turn, would lead to increased cultural connectivity between groups from different regions. Possible drivers of such dynamics are:

(1) Introduction of novel pathogens: inter-species interaction, following a long period of species separation, is likely to have been accompanied by inter-species transmission of pathogens (Greenbaum et al., 2018), which could have caused repeated waves of epidemics, leading to repeated local extinction of groups.
(2) During a period in which territories often change hands, a colonizing group that settles in a new territory, even if it successfully out-competes its preceding occupants, is unlikely to establish. This may be due, for example, to suboptimal physiological adaptation to the environment (in the case of Moderns) or to lack of knowledge of the physical environment. This occurs in non-human animals, and should be expected to have played an even more prominent role among hominins, whose reliance on accumulated knowledge about the environment was likely greater. An example of such a case in recent history is the collapse of a newly-reintroduced Przewalski's horse population in the Gobi desert in Mongolia during a harsh winter. The local wild ass population was able to survive by moving to a valley more hospitable in winter, presumably unknown to the new residents (Kaczensky et al., 2011; see also Jesmer et al., 2018; Keith and Bull, 2017).
(3) Some replacement events may have occurred via direct hostile inter-group interaction, leading to the extirpation of a local group and the utilization of the local resources by the newcomers. It is possible that in many such cases, colonization events were short-lived either due to the culture of the newcomers (e.g., nomads who do not wish to settle) or because the victorious group preferred to search for better territory. This would leave the territory vacant and available for further colonization by other groups.

6.2. Increased contact when something is to be gained

Humans can adjust their rates of interaction with external groups both consciously, following an assessment that such interaction would be valuable, or − if it truly is valuable − via selective processes that act on behavioral or cultural traits that happen to indirectly adjust interaction (Text box 2). Thus, for example, if increased interaction leads to learning new subsistence strategies, individuals may choose to interact and learn from foreigners. A

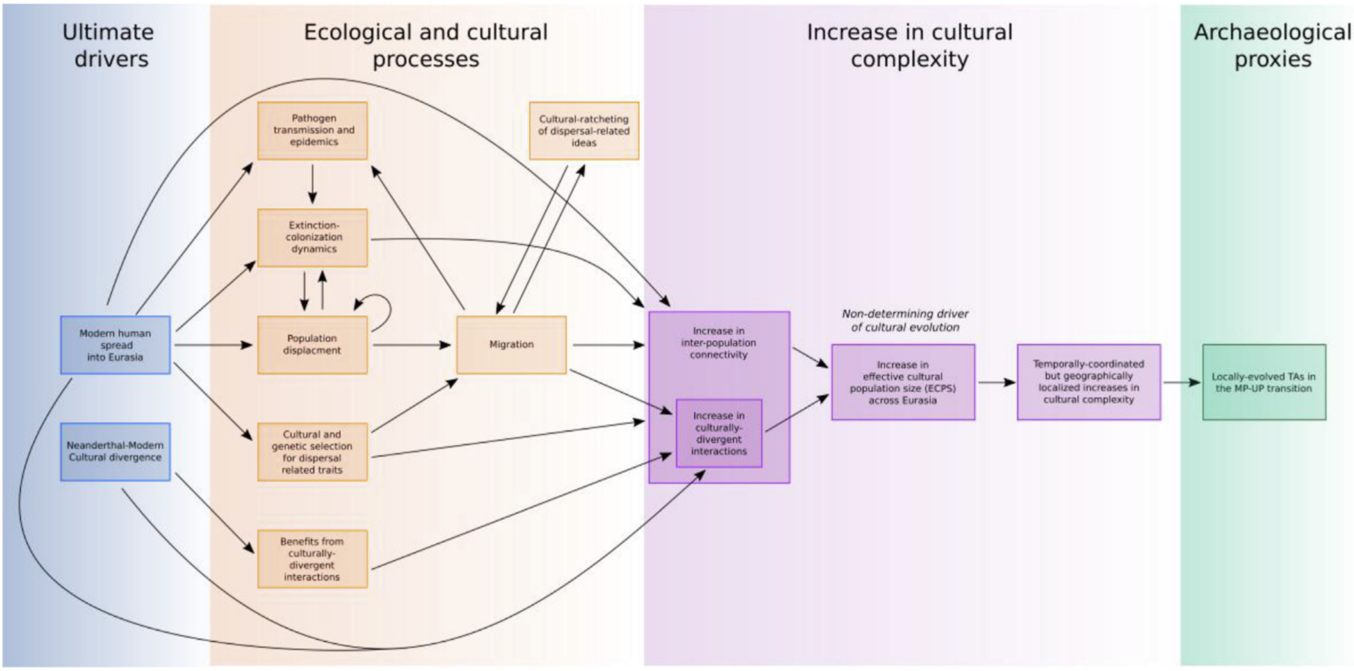

Fig. 1. Schematic and simplified representation of the “population inter-connectivity theory” presented in this paper. The ultimate driving processes of the MP-UP transition are shown in blue; the main ecological and cultural processes we suggest may play a role in increasing inter-population connectivity are shown in orange; the processes leading to locally evolving increases in cultural complexity are shown in purple; the archaeological observation is shown in green. The arrows show some of the possible interactions between the different processes. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

group whose culture encourages out-of-group mating, which leads to increased cultural interactions and cultural gains, would be more successful and outcompete other groups.

When all relevant groups are from the same culture and genetic background (within-species), increased interaction leads to some increase in cultural complexity, but on a timescale that is slow relative to an individual's lifetime, and only to a limited extent. When the groups differ greatly, the novelty that may be learned during the interaction, and the new combinations that can arise from the interaction, may be more salient and realized on very short time scales (Creanza et al., 2017).[9] Thus, in interactions between deeply divergent populations – culturally, genetically, or both – such as is likely to have been the case when Moderns began to arrive in regions previously inhabited only by Neanderthals, groups from both lineages could have benefitted from increased connectivity, more than from inter-group interactions among less divergent groups.

Increased connectivity is advantageous when there is something to be gained; this can be knowledge and ideas, such as new technologies of blade production, but can also be new genes or gene combinations. For each species, introgressed genomic sequences could have provided, advantages in resistance to novel pathogens carried by the other species. Such selective advantage is demonstrated by the over-representation of immune-related genes among the Neanderthal genes carried by many non-African human populations today (Abi-Rached et al., 2011; Enard and Petrov, 2018; Greenbaum et al., 2018; Racimo et al., 2015). It is important to consider, however, that although some Neanderthal genes seem to have conferred immune-related and other selective advantages, others were selectively disadvantageous (Harris and Nielsen, 2016; Juric et al., 2016), suggesting that selection dynamics related to introgression were quite complex (Ding et al., 2014; Racimo et al., 2015).

Importantly, introgressed genes and cultural innovations, even when resulting from inter-species interactions, could have been spread within species via intra-species interactions, once the inter-species transmission had occurred. Thus this driver of increased connectivity may have increased both inter- and intra-species interactions.

6.3. Invasion potential selects for behavior that increases inter-population contact

Currently, the dynamics of invasive spread of non-human species into new regions are being extensively studied, as invasive species have become a major conservation and economic concern (Levine and D'antonio, 2003; Paini et al., 2016). It has been shown that invasion dynamics select for behaviors that produce increased population connectivity, most prominently selection in favor of increased dispersal (Rehage et al., 2016). Thus, for example, in Australia, toads at the forefront of invasion of the species *Bufo marinus*, an invasive species introduced from central America, tend to disperse on average over much greater distances than their counterparts in their region of origin (Alford et al., 2009; Phillips et al., 2010). This is the result of two factors: (1) there are more opportunities, i.e. there is a place previously uninhabited by the species into which individuals can disperse, so more individuals successfully do so, and (2) there is ongoing selection, playing out over longer periods of time, favoring those individuals with a tendency to disperse further or more often.

In humans, such selection might act at multiple levels and via

[9] Interestingly, this prediction is not clearly borne out in the Levantine archaeological record from the late MP, during which Moderns and Neanderthals likely interacted there. As discussed earlier, the record there is characterized by increasing variability in the lithic material toward the very end of the MP, but not a sudden increase in cultural complexity. One possible explanation might be that in this region the increase in interaction between the two groups could have been particularly gradual, playing out over many millennia, thus exerting its effect on culture more gradually than in the dynamics that took place in Europe.

Box 2
Selection and Behavior

In order to understand evolutionary processes, it is important to uncover both the ultimate drivers of selection, and the proximate mechanisms that may facilitate this selection (Mayr, 1961).

In this article, we suggest that certain traits and behaviors related to inter-population contact may have been selected in certain circumstances. While this contact could have been an ultimate cause of the selective process, it leaves open questions related to the proximate mechanisms that would allow it. For example: did selection in favor of increased connectivity act via conscious decision-making by individuals who realized the advantages of contact-increasing behavior in a certain context, or was it driven by natural selection in favor of bands of hunter-gatherers that behaved in a certain way?

The answer to such questions has implications for both the likelihood that the selective process would have been effectively realized via population dynamics, as well as the time scales on which its outcomes were realized. In each of the selective processes discussed in this article, selection might act at multiple levels in parallel, and we assert that in the contexts we propose, selection dynamics at these different levels would usually have been aligned in their directionality. Except where explicitly noted, we leave detailed consideration of the most likely level at which selection might act to future work. Here we lay out four primary routes by which selection is likely to have played a role in the processes we propose.

1. Conscious behavioral choice: Neanderthals and Moderns at the MP to UP transition were cognitively advanced, and were probably characterized by similar reasoning capabilities. Conscious selection of behavior according to its perceived benefits was probably a major determinant of the extent of inter-band connectivity, both within and between the two species. Such decision-making could have been directed explicitly at inter-population contact per se (e.g. "that band has a hunting technique or materials that are worth acquiring"), or culturally mediated (e.g. via encouragement of intra-group mating or taboos that forbid it).
2. Unconscious influence on behavior: Unconscious factors, many of which have deep evolutionary origins, play a prominent role in the determination of human behavior (e.g., Danziger et al., 2011). Such factors must have significantly affected inter-population contact, as drivers of inter-population dynamics that are also targets for natural selection acting upon individuals. Examples are fear of foreigners, curiosity, mate preference that is related to genetic or phenotypic similarity (Penn and Potts, 1999), and genetically-influenced tendencies related to spatial locomotion, risk-taking and migration (see, e.g., Chen et al., 1999; Matthews and Butler, 2011). These factors are shared with many other organisms in influencing inter-population interactions.
3. Natural selection on group-level behavior: when competition between groups (direct or indirect) is intense, natural selection may favor one group over another based on factors that are culturally determined and in which they differ. For example, cultures that favor extreme isolation from other groups may become highly inbred genetically, and more susceptible to epidemics. Similarly, groups that participate more in inter-group interactions may attain high cultural complexity which includes superior means of resource acquisition, and may outcompete neighboring groups that avoid contact and the cross-cultural fertilization that may be associated with it.
4. Selection on cultural traits: selection may act directly on some cultural traits or suites of traits, thus making some more likely to spread than others. For example, a culture, or suite of cultural traits, that facilitates its own transmission (such as in religious missionarism), is more likely to persist and spread than cultural traits that do not prescribe such tendencies.

different routes. One possibility is that groups whose culture was more strongly oriented towards dispersal, expansion, or geographic exploration, were more successful in spreading when the conditions permitted such spread (what these conditions were and what triggered the Moderns spread at this time have been dealt with extensively, yet this remains an open question; see, e.g., Eswaran et al., 2002; Greenbaum et al., 2018; Klein, 2003; Kolodny and Feldman, 2017; Müller et al., 2011; Valet and Valladas, 2010; Wolff and Greenwood, 2010, to name but a few). Such a 'cultural ethos' driver of increased dispersal, and the increase in inter-group connectivity to which it gives rise, can be seen in many historical cases, such as the Mongol expansion throughout Eurasia in the 13th century, or the European so-called "Age of Exploration" in the 15th-18th centuries. Such dynamics are also likely to have played a role in the Bronze-age expansion from the Eurasian steppe (Goldberg et al., 2017; Zeng et al., 2018).

Another way in which increased dispersal may have occurred in humans is via natural selection that favored individuals with a tendency for exploration and for risk-taking behavior. This has been suggested, although it is still hotly debated, as an explanation of today's geographic frequency distribution of the allele of the dopamine D4 receptor across extant populations: the frequency of the allele that appears to be associated with greater novelty-seeking and risk-taking increases among populations, as the distance of the population from Africa increases along inferred routes of Moderns' out-of-Africa dispersal (Chen et al., 1999; Ding et al., 2002; Matthews and Butler, 2011; Wang et al., 2004).

6.4. Cultural ratcheting

Some cultural ideas are more likely to spread than others. For example, ideas that include an element of self-propagation are far more likely to spread than others. Some examples of such cultural traits that have been studied are religions that include a missionary component, or political ideological complexes that include elements preaching the importance of spreading the political complex (Blackmore, 2000; Dennett, 1998; Henrich, 2015).

Ideas related to high rates of dispersal and connectivity are examples of such traits: groups whose culture values increased dispersal will have opportunities to interact with other groups more than those with a more sedentary culture, thus increasing the likelihood that the 'dispersing' cultural trait will spread. The same is true for ideas that favor inter-group interaction, such as the idea of accepting foreigners: an ethos that includes acceptance of foreigners would propagate faster than an ethos of rejecting foreigners, simply because it increases connectivity with other groups, which can in turn adopt this ethos.

In particular, these self-propagating cultural dynamics may interact in a positive feedback loop with the dynamics described above, creating the ‘cultural niche’ that further benefits their spread (e.g., Ihara and Feldman, 2004). Similarly, it may be that once inter-population connectivity is increased, potentially as a response to one of the selective pressures described above, the cultural norms that emerged in order to allow this adaptive response remain and even spread further, regardless of whether the original conditions that fostered the increased connectivity still remain.

7. Conclusions

The MP to UP transition consists of semi-independent transitions that were suspiciously coordinated in timing. We have attempted to explain this *suspicious coincidence* by searching for what we called the *non-determining driver*, i.e. one that determined the timing of transitions but not their cultural content. We propose the *population inter-connectivity theory*, namely that the external, global driver of the MP-UP transition was increased inter-group connectivity, both within and between species. In particular, we suggest that the cultural advancements that have been associated with the MP-UP transition are largely a *product* of the spread of Moderns and their interactions with Eurasian cultures, rather than being the driver of this spread as has been proposed in the past (Gilpin et al., 2016; Klein, 2003; Mellars, 2004; Varki, 2016, 2009).

We focus here on processes of cultural evolution. Alongside this focus, we posit that ecological and evolutionary processes, population dynamics, and the interactions among all of the above, are essential elements whose consideration is paramount to gaining insight into the particulars of the MP-UP transition. We have suggested a number of such factors, which likely influenced inter-population connectivity and cultural interactions: inter-group and inter-species disease dynamics, introgression and the spread of adaptive introgressed genes, extinction-recolonization dynamics, and selection on genetically and/or culturally determined invasiveness-related traits. This study's goal is not to provide a final answer to the questions that are posed, but rather to highlight these questions, to outline the components whose consideration seems important, and to offer a theoretical framework that may be a step towards a better understanding of the MP-UP transition.

Researchers have suggested previously that the emergence of the TAs is related to the spread of Moderns in Eurasia (Hublin, 2015; Stutz, 2015) and that the driver of the TAs' emergence is ‘acculturation’ of local groups by the arriving Moderns (e.g., Mellars, 2004; but see D'Errico, 1998; Tostevin, 2007), or that the cultural changes are an adaptive response to increased competition with the newcomers (Maíllo-Fernández, 2013; Shea, 2003). We suggest that although these forces may have operated, it may be productive to interpret the archaeological record of this period in light of explicit models of cultural evolution and in light of insights from empirical examples of cross-cultural interaction or of cultural interactions in structured populations. These suggest that cross-cultural interactions, even among initially-competing and hostile groups, can be culturally constructive, i.e. they give rise to novel inventions, ideas, and potentially whole suites of traits, that did not exist previously in either culture. These interactions are often two-way interactions, with both cultures contributing to the emergent outcome.

This perspective suggests that the assumption that each TA was uniquely associated with a single species may be incorrect. The record suggests that the cultural and demographic dynamics of the MP-UP transition were local and complex, between cultures that changed dynamically over the course of this transition period, at least in some regions. Thus, the assignment of a local culture to one species or the other does not contribute much to a general understanding of this period. Such an attribution would be insightful only if a culture were stably associated with a single group or species along time and space, marking its range expansion or retraction with respect to other groups or species. This could be the case for some TAs, perhaps the Emiran for example, but not for others.

Similarly, assigning technological elements as derived from the culture of one species or the other may often be unproductive, considering that Moderns and Neanderthals are likely to have interacted in the Levant for millennia prior to the Moderns' spread throughout the rest of Eurasia. An advanced culture emerging from such an interaction should be attributed to both “parental” cultures and is expected to differ from both. The time span during which the MP-UP transition took place was sufficient for the emergence of cultures that were hybrid products of cross-cultural interactions, in some cases between cultures that themselves emerged in a similar manner within this period. Flagging particular elements as distinctive of one of the cultures-of-origin or another may often be unwarranted, if the reality was truly as complex as we suggest.

A line of evidence that could support our theory, although not necessarily ruling out alternatives, would be evidence of increased connectivity among groups associated with the TAs, particularly near their emergence. Multiple proxies may allow some assessment of connectivity rates, although each is obviously quite partial: mean distance of procurement of lithic material; isotopic analysis of skeletal remains that might suggest long-distance migration within the lifetime of the individual; isotopic analysis of animal remains that may have been carried around, such as bone tools, which begin to appear stably near this time period; distance of shells from their place of origin. These have been studied in many instances, and overall do imply an increase in connectivity in the UP compared to the MP (e.g., Bar-Yosef, 1998; Ekshtain et al., 2017; Féblot-Augustins, 1993; Féblot-Augustins, 2009; Tomasso and Porraz, 2016; Vanhaeren and d'Errico, 2006). Further analyses along these lines, coupled with increasingly powerful analytical tools, may allow characterization of these patterns of connectivity at greater time and space resolutions, which could help to evaluate whether the changes in connectivity are merely a product or a prominent driver of the cultural transitions between the MP and the UP. Another topic for future exploration is the details of the interactions that may have taken place: here, we have discussed multiple types of inter-population interactions, suggesting that their effects are largely overlapping. However, it is reasonable to expect that greater connectivity across regional interaction networks might have somewhat different effects from those of increased connectivity following occasional large-distance migration events.

The transition from the MP to the UP, which occurred along different routes in Eurasia, was perhaps one of the most exciting developments in hominin history. We view this transition as a dynamic process of cultural evolution that occurred in complex, highly structured, cultural and demographic contexts, both in space and in time. This view emphasizes joint considerations of ecological, demographic, evolutionary, and cultural-evolutionary dynamics, in order to better understand the transition. A study of commonalities and differences in the ways in which the transition occurred in different localities and a search for general principles underlying these processes may be a productive path towards a better understanding of this crucial period.

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