Research

The evolution of the diversity of cultures

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The abundant evidence that *Homo sapiens* evolved in Africa within the past 200 000 years, and dispersed across the world only within the past 100 000 years, provides us with a strong framework in which to consider the evolution of human diversity. While there is evidence that the human capacity for culture has a deeper history, going beyond the origin of the hominin clade, the tendency for humans to form cultures as part of being distinct communities and populations changed markedly with the evolution of *H. sapiens*. In this paper, we investigate ‘cultures’ as opposed to ‘culture’, and the question of how and why, compared to biological diversity, human communities and populations are so culturally diverse. We consider the way in which the diversity of human cultures has developed since 100 000 years ago, and how its rate was subject to environmental factors. We argue that the causes of this diversity lie in the distribution of resources and the way in which human communities reproduce over several generations, leading to fissioning of kin groups. We discuss the consequences of boundary formation through culture in their broader ecological and evolutionary contexts.

Keywords: culture; human evolution; human diversity; cultural evolution

1. INTRODUCTION

In evolutionary terms, if culture is the way in which humans deploy their behaviour through socially learned means, then it could be said that there is only one culture. As other papers in this volume show, the capacity to be at least a limited culture-bearing animal has deep roots in the hominoid clade, probably evolved convergently in other mammalian species, and evolved during the course of hominin evolution over a period of several million years [1]. The concept of culture has become increasingly part of the evolutionary toolbox [2], but the use of ‘culture’ by evolutionary biologists remains only a fragment of the anthropological range. While ‘culture’ is the cognitive system which enables us to generate much of our behaviour, and presumably ultimately involves a set of biologically based cognitive processes, the product is something else entirely. The human capacity for culture has resulted in enormous diversity at the population level, so that we can recognize that the way in which humans form cultures is as important, in evolutionary terms, as the capacity for culture itself. So, while at the species level there may have been the ‘evolution of culture’, once in place we need to consider an entirely different question—why are there so many different ‘cultures’? The answer we will propose is that cultures were and are the outcome of the way in which kin-based human communities reproduce themselves over generations, and in doing so fission; that the rate of fissioning is strongly influenced by

ecological and geographical factors; and that humans have a unique cognitive capacity to generate socially transmissible behaviours which structure the outcome of the fissioning. The result is the formation of boundaries between human communities; cultures are the consequence of these group boundaries, and boundary formation is perhaps the central and most important element of the evolutionary ecology of culture. The diversity of cultures derives from the intersection of species-specific cognitive capacities with demographic and ecological conditions over the past 100 000 years. In particular—in contrast to biological processes—it is the way in which that capacity for culture generates behaviours with low within-group variation and high between-group variation that has underpinned the success of the species.

2. CULTURE AND CULTURES

We consider, following Boyd and Richerson [3], the capacity for culture to be a species-specific trait, in which the human brain produces mental states which process, transmit and receive information ‘capable of affecting individuals’ behaviour that they acquire from other members of their species through teaching, imitation, and other forms of social transmission’. One of the primary outcomes of the capacity for culture is particular sets of behaviour, mostly homogeneous within populations, and different between them. Culture, therefore, produces ‘cultures’. Individuals in close social proximity adopt behaviours which are similar to each other and different from others. Cultures, for the purpose of this paper, therefore, are communities with shared behaviours, and we would argue that although other types of cultures can and do occur, they have in

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One contribution of 26 to a Discussion Meeting Issue ‘Culture evolves’.

Figure 1. Comparative genetic diversity of apes and humans. The horizontal bars indicate the range and average pairwise difference between individuals in mtDNA sequence; the cartoon on the right is an unrooted tree of the ape/human clade, based on mtDNA, in which the branch lengths are equivalent to sequence divergence. Modified from Gagneux *et al.* [9].

evolutionary terms been isomorphic with kin-based reproductive communities, and thus populations in the biological sense [4]. In contrast to other discussions about cultural diversity [5–7], we are interested in the diversity of these communities, as ethno-linguistic groups in all probability, rather than the cultural traits which define them and are propagated by them. We therefore distinguish between cultural diversity (which refers to the way in which socially learned traits diversify and spread), and the diversity of cultures, which refers to the populations or communities which are the reproductive vehicles for cultural traits, and which are the evolutionary beneficiaries (or, conversely, losers) of their adaptive values. In this context, this paper is more concerned with the communities as social and biological units (diversity of cultures), than the specifics of their cultural attributes (cultural diversity).

Communities are, of course, notoriously difficult to define, and have few fixed boundaries. For many reasons, individuals move from community to community during their lifetime, and may belong to more than one. Communities may also be nested one within another. We may consider Kenya to be a community as a nation, but it is also a series of communities defined ethno-linguistically—Kikuyu, Turkana, etc.—and even within those, further kin-based clans and groups occur. Fissioning and subdividing seems to be an integral part of the process of culture formation, and so cultures must also be defined as multiscale.

Cultural communities form the bedrock of human organization and diversity [8], and it is our argument here that the process of the diversification of human communities involving cultural behaviours is an essential part of the human evolutionary story. Structured, comparatively invariant, human cultures provide many of the great strengths of human adaptation—the products of the processes of conformity; they also often lie at the heart of human conflict. In summary, an aim of this paper is to ask why are there so many human cultures and how did they come to develop?

3. HUMAN DIVERSITY: A BIOLOGICAL AND CULTURAL PARADOX

One obvious answer to the question about the scale of the diversity of human cultures is to posit that it reflects the scale of biological diversity. Humans are a vast population, spread across the whole globe, and living in many different environments. It could therefore be expected that large numbers of human cultures would reflect high levels of biological—or more specifically, genetic—diversity. However, this is not the case. The human species is a young one, descended from a small population that lived in Africa between 150 and 200 kyr ago. As a result, the human species is genetically not very diverse. Measuring genetic diversity can be done in a number of ways, but a simple one is to compare sequence diversity in mitochondrial DNA across species. Figure 1 shows for species and subspecies of great apes and humans that the latter have the lowest level of diversity, reflecting the short time-depth of human populational origins [9].

Any attempt to compare cultures across species in a similar way is doomed, as the scale of difference is too vast. Humans are genuinely unique in the rate at which they can generate differences between communities, even if there are primate homologues for the capacity. The Ethnologue records some 6909 extant languages [10]. Price's Atlas of Ethnographic Societies [11] records over 3814 distinct cultures having been described by anthropologists, certainly a major underestimate. In practice, given definitional problems and a state of constant flux, a precise number cannot be calculated. However, another way of considering the problem is to calculate that if all the world's languages were evenly distributed across the habitable world, then, on average, a journey of only 78 km would bring a traveller from the centre of their language territory to a language boundary. A journey of 1000 km would, on average, pass through over six language territories. The traveller across the same distance would

be less able to distinguish major phenotypic differences, and would see few marked boundaries. Languages are more widespread than cultures, in most cases, so the rate of changing culture would be even faster. These areas and distances are well below the resolution for geographical ancestry estimates based on genetics.

These are gross generalizations, and exceptions can be found where biological boundaries are abrupt and clear-cut, and cases where cultural boundaries are diffuse. Also, the areas occupied by cultures vary environmentally [12–15], and so the distances may well be smaller or larger. Nonetheless, this broad generalization is sufficiently true to allow us to explore the paradox of low biological diversity and high numbers of cultures, in terms of the processes of cultural diversification.

The relationship between biological and cultural diversity can be examined through its structure. According to Lewontin [16], approximately 85 per cent of the genetic variation observed in human populations occurs within, rather than between populations [16]. Although out of date, Lewontin’s analysis of variance remains a relevant observation about genetic variance. His analysis was pre-genomic, and based on single loci considered independently. Molecular data and multiple loci have greatly modified Lewontin’s observation [17,18], but it remains the case that there is considerable variation within all human populations and communities, certainly at larger geographical scales.

What happens when we turn to cultural diversity and ask the same question about intra- and inter-population variation? It is obvious that cultural variation should be partitioned very differently, for what constitutes a culture is the sharing of behavioural, social and material traits, and these are different between cultures [19]. Cultural diversity can virtually be defined as between populational behavioural variation (figure 2). Of course, it is not the case that every member of a culture is behaviourally identical, and in practice a culture is made up of individuals each of whom has a different combination of behaviours, in the same way as each individual in a population has a unique combination of genes. One of the main differences between genes and cultural traits is the within-population frequency of variants, with cultural variants being mostly more homogeneous within than between groups in their expression. It is this difference that allows us to draw cultural maps as territories far more easily than we could with biological markers.

The key point is that both biological and cultural traits reside in individuals, but take on a population-level character which is both shaped by and shapes evolution. Both types of trait vary within and between populations, and can be described in frequency terms, but their structure is very different, and so acts differently in adaptive terms. Selection for generating and/or maintaining different cultures is nothing more, in a way, than strong pressure for fixation of behaviour within groups. The remainder of this paper will consider how this diversity of cultures has developed—the pattern—and the processes by which it is structured.

	intra-population variation	inter-population variation
human genetic diversity	high	variable
human cultural diversity	low	normally high, but can be low

Figure 2. Characterizing the structure of human diversity. Genetic, and to some extent phenotypic biological, variation has been shown to be highly variable within populations, and less so between them; in contrast, the key trait for cultural variation is that it is normally very low within a population, but high between.

4. PREHISTORY OF THE DIVERSITY OF HUMAN CULTURES

(a) *Evolution of Homo sapiens: constraining cultural evolution*

The paradox of low biological diversity and high cultural diversity among humans can be used to provide us with a basis for considering the origins of community-based cultural diversity. A variety of genomic markers place the demographic origin of *H. sapiens* towards the end of the Middle Pleistocene, somewhere between 200 and 150 kyr ago [20]. Different genetic markers provide slightly different estimates, but this is a broadly robust conclusion [21]. For mitochondrial DNA, the older genetic lineages (i.e. haplogroups such as L in the current terminology) have an origin (i.e. coalesce) at around 100 kyr ago [20], and there is a suggestion that the genetic diversification of the major geographical groupings of the human population known today occurred between then and 60 kyr ago [22]. This does not exclude other and earlier populational lineages, none of which have persisted through to the present day. These results indicate an African origin for the species, with most current human diversity developing after 100 kyr ago.

This information is broadly consistent with the fossil record, although the latter is despairingly sparse for much of the period [23]. Omo Kibbish, in Ethiopia, shows a ‘modern’ if very robust morphology at 190 kyr ago [24]; Herto, also in Ethiopia, at 160 kyr ago [25], is also ‘modern’ in certain key anatomical attributes, although does not fit obviously within extant variation. Apart from these early specimens, the African fossil record is scant; Klasies River Mouth (South Africa), Skhul and Qafzeh (Israel, but biogeographically African) occur around 100 kyr ago; and until the end of the Pleistocene the only African specimens of note are Aduma (Ethiopia) and Hoffmeier (South Africa); these are either not very informative, or else do not relate strongly to extant regional populations. Outside Africa, modern human fossils are present from

at least 40 kyr ago in Australia, 45 kyr ago in South-East Asia, and at roughly similar times in North Africa, the Middle East and Europe (see [26] for summary of later Pleistocene record). Overall, the fossil record indicates a much earlier presence of modern humans in Africa than elsewhere, weak links with local recent populations, and a much later appearance outside Africa.

In terms of evolutionary population history and the diversity of cultures, the genetic and fossil evidence allows us to say that the clock essentially starts no more than 200 kyr ago, and most probably at a much younger date (less than 100 kyr ago).

(b) Phases in the evolution of the diversity of cultures

From this starting point towards the end of the Middle Pleistocene a number of informal phases can be identified, which provide some insights onto the way in which human populations diversified culturally.

(i) *Phase 1: anatomical modernity and cultural continuity*
Although the earliest fossil specimens which have been referred to as anatomically modern occur between 200 and 150 kyr ago, on the basis of archaeological evidence one would be hard pressed to identify any change in the patterns of cultural diversity or the propensity for cultural differentiation at this time. The transition from archaic to modern humans is characterized by the continuation of Mode 3 technologies (i.e. the prepared core technology which defines the Middle Stone Age (MSA) of Africa and the Middle Palaeolithic of Europe, as found in both European and African lineages [27]). Prepared core/flake technologies occur considerably earlier, possibly as old as 300 kyr ago, and possibly involve a number of innovations in behaviour (use of ochre, for example) [28], but continue unchanged throughout the anatomical transition [27]. The implication is not necessarily that there is no diversification of community-based cultures, as it can be argued that these are of considerable antiquity and existed in some form in the last common ancestor with *Pan* [29], but that the rate and material group marking do not change substantially. Anatomy precedes evidence for changes in cultural diversification.

(ii) Phase 2: the African MSA, ephemerality and regionalism

Contrary to much earlier writing, it is now fully recognized that the evolution of modern humans is associated with the MSA or Mode 3 technology, rather than the Upper Palaeolithic and Mode 4 or blade industries [27]. However, it is also becoming clear that the MSA is not itself homogeneous. The early parts are very poorly dated and understood, but recent research has shown that what can be considered the classic or later MSA probably occurs from approximately 120 kyr ago. This phase of the MSA is characterized by a much greater degree of regional variation, shown in the presence of both particular patterns of lithic reduction—for example, the microliths of the Howieson's Poort industry—and particular end forms or tool types (the Aterian tanged points of North Africa, the delicate Stillbay bifacial points in

South Africa, for example). Associated with this phase is also the first evidence for body decoration (beads) [30–33] and for intentional marking which has been interpreted as 'symbolic' [34]. It can plausibly be argued that what is emerging here is a greater pattern of populational differentiation based on behaviour. Stone tools can probably only be a crude reflection of this, but this phase (from 120 to 50 kyr ago) reflects the cultural differentiation of the first modern human populations as they dispersed across Africa.

More detailed chronological studies have added a further twist to our understanding of this period. Jacobs *et al.* have shown that the Howieson's Poort is in fact a short-lived (5 kyr) flourishing of a particular cultural entity, not part of any prolonged trend [35]. This ephemerality, most probably also for the Stillbay, could indicate the sort of short-lived rapid expansion and decline associated with cultural markers and their host populations which is central to notions of cultural evolution and diversity.

(iii) Phase 3: the diversification of human populations in the Old World

Prior to approximately 50 kyr ago there is no substantial evidence for modern humans outside Africa (with the exception of the sites of Skhul and Qafzeh in the Levant, and there are grounds for considering this to have been part of the within-African dispersals, and ephemeral). Beyond this date, human populations were clearly larger, genetically more diverse, and became widespread in Eurasia, and, indeed, had dispersed into Australia [22,36]. By this stage, evidence for the 'diversity of cultures' is substantial. The existence of regional traditions noted in the African MSA becomes even more marked in the Upper Palaeolithic and LSA; this is typified by the marked increase in the number of regional 'cultures' (in archaeological terms) which appear, and are characterized by differences in both lithics and more stylistic features—figurines, bone points, harpoons, beads and so on. These persist for only a few thousand years (much shorter than those of the MSA). The best known of these are units such as the Aurignacian, Gravettian, Solutrean, Wilton, Kenya Capsian and Eburran, but in all probability there are many more. There seems to be little doubt that by 40 kyr ago, in Europe at least, culture-based community differentiation was occurring, probably in ways very similar to those observed ethnographically. Vanhaeren and D'Errico have demonstrated in a very elegant and detailed analysis of the morphology of Aurignacian beads that the pattern of variation is best interpreted as ethno-linguistic groups across Europe [37]. Sadly, other parts of the world do not have a sufficiently complete record to recognize similar patterns. Beads and stylized decoration on ostrich eggshells in Africa during Phase 2 [38] may indicate that, albeit demographically less stable, Phase 3 of cultural differentiation only represents the Eurasian magnification of what was already taking place in Africa.

(iv) Phase 4: climate, environment and fragmentation

There is little evidence to suppose that after 50 kyr ago there has been a significant genetically based change in the capacity for humans to express themselves

culturally, and so in one sense one might expect that the pattern in place by Phase 3 simply continues. To some extent, in terms of process, it does. However, the period after 25 kyr ago shows a new intensification. Again, Europe, with its much richer archaeological record, provides the clearest evidence. The archaeological evidence shows an increase in the level of regionalization, and also a much greater elaboration of traits which can be described as having a primarily social function (e.g. cave art). One example is burials from Sunghir, where the three corpses were covered with more than 13 000 beads; another would be the extraordinary proliferation of art in the Magdalenian; and yet another is the existence of epi-Palaeolithic social territories in the North German plain in the Late Pleistocene [39]. The most probable explanation is that this is an effect of climatic deterioration (the last glacial maximum), leading to fragmentation of populations, isolation and intensification of group-based processes and identity [40]. In effect, this phase shows that the diversity of cultures is likely to reflect demographic and ecological processes [41], and possibly ones where the option of spreading risk by reducing boundaries [12] is not viable because there may have been genuine isolation of small populations. However, major resource pressure can also lead to opposite strategies—the formation of very low density, very mobile groups which cover very large territories. These latter would benefit from decreased cultural boundedness and increased small community inclusivity, and may underlie the homogeneity of the Australian prehistoric record of the time [42]. These regional cultural trajectories set the different starting points for the subsequent phase of economic intensification.

(v) *Phase 5: post-Pleistocene complexity and the growth of intensive economies, cities and empires*

The end of the Pleistocene was shaped by climatic amelioration which started around 14 kyr ago, and with this came innumerable changes in human demography and adaptation. The first changes were the dispersals of hunter–gatherers, seen worldwide (e.g. the African LSA, the European Mesolithic or the colonization of America) in response to warmer conditions, which in parts of the world, led to the development of food production and domestication. At this point evidence for the diversity of cultures increases very significantly. This is a mixed pattern; on the one hand, some of the dispersals associated with agriculture led to a homogenization in the first instance, with closely related cultural and linguistic communities spreading widely—in Africa (Bantu), in Europe (Indo-European) and across the Pacific (Austronesian) [43]. On the other hand, this also resulted in the fragmentation of indigenous groups, with highly diverse communities existing in a complex palimpsest in many parts of the world. Large-scale population dispersals and subsequent reduced contact resulted in rapid and extensive differentiation (1231 Austronesian languages developed in less than 5000 years, and 522 Bantu ethno-linguistic groups in Africa) [10]. The development of cities, states and empires both

enhanced this process, but also, with growing economic and military differentiation, led to a reduction in diversity through extinction and absorption. The result is human landscapes which are complex, with diverse communities existing in a patchwork of overlapping territories or cultural units.

(c) *Pattern of cultural evolution*

What does this brief review of the history of the diversification of cultures show? It can certainly be argued that there is, in the human phenotype, an inherent capacity for communities to diversify and to mark this culturally. There is no reason to suppose that non-modern communities may not also have shared this capacity. However, we would be hard pressed to identify this in the earliest phase of *H. sapiens*. From very approximately 120 kyr ago, we see much greater evidence for the process of the diversification of cultures, first in Africa, and then elsewhere. The rate, however, is not constant, neither through time, nor in relation to climate, environment and demography. Furthermore, we would argue that this early process of diversification is intimately related to the diversification of biological populations, and so language and culture do map broadly on to genetic diversity, but that later dispersals and extinctions have blurred this correlation. However, as discussed above, the structure of this diversity is very different, and this allows us to consider in more detail the processes through which the evolution of the diversity of cultures takes place.

5. DETERMINANTS AND OUTCOMES OF THE DIVERSITY OF CULTURES

Having briefly considered the history of patterns of cultural differentiation, two broad issues emerge: the first is the question of what the underlying causes of community differentiation based on cultural traits are, and the second, the consequences for human populational structure.

(a) *What leads to the diversification of culturally defined communities?*

Determining causality in evolution, especially where humans are concerned, is never simple or uncontroversial, partly because one has to be precise about the nature of the causality proposed (proximate versus ultimate mechanisms, for example), and partly because of a reluctance among anthropologists to accept causal relationships of large issues such as culture. We are concerned here with two very precise elements. One of these is the way in which ecology and the environment more broadly affect the rate of community differentiation—in effect, closely related to Tinbergen's functional question; the second is that cultural diversification arises, almost inevitably, from the reproductive life history of communities. We do not address here, although inevitably assume, that there are underlying proximate cognitive mechanisms which interact with these broader demographic and ecological factors.

(i) *Resources, ecology and environment*

The distribution of human cultures has been the subject of considerable recent research; a number of

Figure 3. Relationship between cultural density (the number of populational cultures per unit area) and rainfall (top) and temperature (bottom). Modified from Collard & Foley [14].

studies have shown that, both regionally and globally, the distribution is not random, but rather strongly influenced by environment. Birdsell [44] was among the first to show this for Australia; in the past decade or so, similar patterns have been shown for languages globally [12], within Africa [15], in North America [13], and for cultures globally [14] and in relation to political complexity [45]. In broad terms, the pattern found is one that replicates many of the species–area relationships for other mammals, with greater diversity in tropical regions and in areas with high productivity. Latitude, temperature and rainfall are all good predictors of the ethnographically observed diversity of cultures (figure 3). A number of proximate mechanisms have been proposed—for example, that the formation of boundaries between groups is promoted by resource reliability and reduced where variability and associated risk is such that it pays to maintain relationships across communities.

There are a number of ways of phrasing a resource-based hypothesis for the diversity of human cultures. The most parsimonious is to think in terms of the probability of boundary formation. Human cultures, as communities of individuals, form when boundaries begin to occur within such communities, and when, through both adaptive and neutral mechanisms, the traits of each community—from language to decoration to technology—begin to diverge. Where individuals and ideas can flow across such potential boundaries, then the probability of divergence is reduced. In essence, the formation of boundaries,

and so different cultures, is an outcome of the context; this may be the natural context, where there are real geographical barriers, or demographic ones, where there may be competition. In either case, diversity of cultures is basically being driven by resource availability and its social and economic context [46]. The boundary formation, or lowering of interaction rates, results in a (rapid?) move towards fixation of some cultural traits in each daughter community. If we turn back to the evidence for the development of this pattern during the Pleistocene, we can note that the changing climatic and demographic conditions of the past 120 kyr are likely to have influenced the rate of boundary formation, and thus produced geographical patterns different from those seen today. The underlying ecological causality, however, would remain the same. This is a simple proposal which would hold for the longer phases of expansion of human populations and major dispersals; however, under some circumstances, there may be intense boundary formation as part of a process of local intensification, despite there being continued interaction [47].

(ii) *The life history of a community: kinship and reproduction*

If ecology and resource distribution shape the variation in rate and probability of boundary formation, other factors which make it probable that communities will diverge, even in the most unfavourable of conditions, need to be considered.

It was asserted at the outset that a culture was multiscalar, and can be anything from a nation to a local clan. Much recent theory has focused on how virtually any group may form a subculture or a cultural variant. However, for the largest proportion of human history and prehistory, and certainly for the context in which humans evolved, communities would have been local reproductive units, based on kinship, probably built around a descent group. We have argued elsewhere that this form of community is likely to be the fundamental unit of human sociality, and probably homologous with the chimpanzee community [4,8]. When we talk, therefore, of the evolution of the diversity of cultures, what we are interested in is communities such as these, and how they develop their own identity.

If most aboriginal human communities were based broadly on descent groups, then descent traced from a single ancestor community would be tree-like through the generations. Over a relatively small number of generations, such a community would have more and more descendent reproductive units, less and less closely related to each other. Fissioning of these communities, and often physical movement into other areas, is an inevitable consequence of the life history of any descent groups and has been central to classic anthropology. Over time, descent and divergence will lead to the fissioning of communities and the formation of separate ones, with adaptive and demographic consequences [48]. As this process occurs, cultural norms and behaviours develop which hold these communities together, such that the outcome will be both cultural and biological diversity. This process—what we are referring to here as the life history of descent groups—underpins the diversity of cultures.

(b) What are the outcomes of a tendency to form cultures?

Given three key elements of the process of cultural differentiation—(i) that human communities have a tendency to diverge as a product of how biological and social reproduction develops over several generations, (ii) that the species as a whole exploits this tendency through cognitive systems which mark differences between communities, and (iii) that the rate of such fissioning is ecologically and demographically sensitive—we can ask a further question, namely how these processes, operating together, have structured the diversity of culture on regional and global scales.

(i) Phylogenetic relatedness in culture and biology

Perhaps the most significant outcome of the processes described here is that, for the most part, the more similar two cultures are, the greater their geographical proximity. There has been some debate about the role of ethnogenesis versus phylogenesis in the formation of new communities [49], but, as described above, the overall pattern, the broad regional social areas, would indicate that the formation of new cultures normally occurs through two communities fissioning adjacent to each other. Subsequent dispersals, extinction and other such processes, may well blur this pattern, but phylogenesis is the basis for the fact that linguistically and culturally it is possible to identify affinities

across continents at least. As, by definition, genetic systems must descend and diverge in this way, and as reproduction will, even for autosomal genes, tend to follow this pattern, then there should always be a strong pattern of co-variation between biological and cultural relatedness at this broad level [50]. To that extent, the history of the diversity of human cultures will also be the history of human populations as they have formed, moved and died out, and there will be a relationship between biological and cultural phenotypes.

(ii) Regional diversity

If phylogenesis drives the diversification of communities, and with it biological and cultural differences, then patterns of regional diversity are the outcome. However, these are not the same across the globe. The frequency of cultural and populational differentiation relates to the probability of a boundary, natural or social, forming between two communities. Elsewhere we have shown this to be strongly influenced by two factors—the probability of isolation, and the variance in resource availability between habitats [46]. High levels of diversity of cultures are more likely to occur where there is a high probability of geographical isolation, and where there is a high gradient in resource availability between habitats, or both (figure 4).

(iii) Extinction

In developing the ideas here about the diversity of cultures, emphasis has been on the inevitable proliferation of cultures as communities reproduce, grow and adapt. It might be expected that there would simply be a continuous and endless process of cultural expansion; however, the recurrent recognition that there are environmentally driven patterns across many regions suggests that actually there is at least a partial state of equilibrium in the diversity of cultures. For an equilibrium to occur then there must be a balancing process of ‘extinction’. Archaeologists have done much to map the comings and goings of archaeological cultures, but much remains to be done to see how these relate to the processes described here; however, the expansion of western populations in the past 500 years, with the consequent loss of languages, cultures and populations, shows that it is a powerful force.

However, it is not the rate or power that concern us here, but the impact on the structure of diversity. According to the model of gradual phylogenesis by fissioning proposed above, across a landscape there should be a general pattern of continuity between communities, cultures and populations; however, should extinction occur at points along this continuity, and should there be subsequent expansions, then the overall structure will consist of a series of related communities, with a few outliers occurring. In practice, this is a situation seen very frequently throughout the world—non-Bantu in a sea of Bantu-speaking cultures in Africa; Papuan isolates in a continuum of Austronesian speakers; Basques among the Indo-Europeans, and so on. The extinction of groups, with their languages and their cultural traditions, structure regional diversity.

Figure 4. Relationship between environmental gradients and isolation in rates of group-boundary formation (i.e. formation of diversity in cultural units). Environments may have high or low probabilities of forcing populations to become isolated, and they may also have either large or small habitat differences in resource availability and richness. The former will determine the rate of boundary formation due to drift and isolation; the latter the rate of boundary formation due to competitive fissioning. Modified from Foley [46].

What is perhaps most significant, however, is that this is where mismatches between genetics and culture will begin to occur; cultures may well disappear, because they are complex, made up of multiple traits and require large groups to survive; genes, on the other hand, can slip through such events on an individual basis and as part of a survival strategy of the individuals themselves. Genetic lineages, therefore, are likely to be older and more persistent than cultural ones.

6. CONCLUSIONS

(a) *Individual strategies, group norms, biology and culture*

The evidence summarized here suggests that the diversity of human cultures is a specific outcome of the way in which human populations have expanded and dispersed since the origin of the species. Lineage-based communities will fission over time, and the result will be divergence and the formation of boundaries. The rate of fissioning and boundary formation will be ecologically and environmentally sensitive, and local demography will play a major role. While this process is likely to occur in many species, humans bring to it a particular cognitive ability, namely a very high rate of socially transmitted behaviours across a whole realm of activities. The adaptive nature of many of these is one element, but both adaptive and neutral components will have consequential effects on diversification of populations. In particular, it is the capacity of socially transmitted behaviours to retain within group homogeneity—and between group differences—that underlies the links between biological and cultural differentiation.

Two points might seem to emerge from this discussion—one, that culture is simply tracking biological diversity, and the second, that while genes belong to individuals, cultures belong to groups. While there is an element of truth in both these points, it is the differences from them which are more interesting. First, while there is a regional co-variation between culture and biology, phylogenetically, ecologically and demographically, it is more probable that patterns of genetic diversification are following cultural packages, rather than the other way around. Culture, in this sense, constrains biological diversity. Language, beliefs and other customs strongly influence mate choice, and so the transmission of genes. Second, while it can clearly be demonstrated that genes belong to individuals, the converse—that cultural traits belong to groups—does not necessarily follow. In practice, each individual carries around a suite of cultural traits, usually in the context of many other individuals who will share them. However, an individual can deploy his or her suite of such traits in many different ways, including abandoning them completely in favour of others. As such, individuals can further their genetic interest by manipulating their cultural traits—hence confusing further the relationships between biology and culture. Individuals exploit ‘cultures’ for Darwinian purposes.

(b) *What advice should we give the culturally ambitious chimpanzee?*

Finally, this paper has focused entirely on humans, and more specifically modern humans, with no references to a broader hominin or hominoid comparative

context. Given the presence of many aspects of 'culture' in pre-human hominins, and among some of the anthropoid apes, it might be asked why do these species not diversify at the same rates, and create the same rich patchwork of culturally diverse communities? The odd variation in chimpanzee handshakes does not compete with more than 6000 different ways of saying hello [51]. To answer that question would be to specify the conditions under which human evolution took on its unique trajectory.

On the basis of the argument developed in this paper, there are three avenues to be explored. One could be that chimpanzees and early hominins simply lack the cognitive capacity to generate sufficient behavioural variation which can be transmitted, retained and observed. Without that cognitive skill, the persistence of cultural traits, their maintenance within lineages, might not be possible and so 'cultures' die out at a faster rate than they are generated.

A second possibility is that diversity of cultures requires certain environmental and ecological conditions. A high rate of boundary formation required a high gradient of environmental difference, and also a potential for isolation by distance. It is possible that chimpanzees and early hominins inhabit environments lacking the conditions necessary for such diversification, or, as Shennan has suggested, habitats which do not support sufficiently high population densities.

The third proposition lies in the way in which communities developed and fissioned. In practice, human communities will make contacts and alliances even after divergence, often through marriage, and often to maintain sufficient military strength. There is increasing evidence that chimpanzee males are unremittingly hostile to members of other communities [52], and this lack of ability to moderate conditionally inter-group encounters may, ironically, be what inhibits high levels of chimpanzee cultural diversity.

Whichever is the case, the similarities and the contrasts between humans and chimpanzees are essential for understanding the conditions under which humans have proved to be capable of generating diversity of community behaviours on an unprecedented rate.

The research reported here was partially supported through many research grants from NERC, UKIERI, Eurocores, the Isaac Newton Trust, the King's College Human Diversity Project, and the Leverhulme Trust. We thank Federica Crivellaro for discussions.

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