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The cultural wealth of nations

Mark Pagel and Ruth Mace

Why, when the human race shows comparatively little genetic variation, are cultural differences so widespread and enduring? Thinking about cultures in terms of biological species provides some provocative answers.

umans are the virtuosos of cultural diversity. We fish, hunt, shepherd, forage and cultivate. We practise polygyny, polyandry and monogamy, pay bride-prices and dowries, and have patrilineal and matrilineal wealth inheritance. We construct or inhabit all manner of shelters, speak about 7,000 different languages and eat everything from seeds to whales. And this is not counting many unique, and sometimes bizarre, belief systems and behavioural practices¹.

Contemporary cultural diversity is probably a fraction of the diversity that has ever existed, and there may be less cultural diversity now than there was 10,000 years ago, just before the advent of agriculture. Because of their superior reproductive rate, agriculturalists replaced many indigenous hunter-gatherer cultures as they spread across Europe and other parts of the globe^{2,3}.

If the picture of human cultures is one of variability, the human genetic landscape is one of homogeneity. All of humanity varies less genetically than does a typical wild population of chimpanzees^{4,5}. This may reflect our youthfulness as a species. Anatomically modern Homo sapiens emerged only about 75,000-100,000 years ago, and may have suffered a demographic 'bottleneck' in the recent past, meaning that in evolutionary terms we are all descended from a not-sodistant common ancestor. Also, of course, we can interbreed throughout our entire worldwide range. Add the facts that we regularly trade, migrate across each other's territories and wage war against each other, and a puzzle emerges: where does our extreme cultural diversity come from, and what maintains it?

The answers can perhaps be found in thinking about human cultures as if they are collections of distinct biological species. Just as species carry genetic adaptations to their environments, we believe that cultural adaptations have evolved in response to social life, and that such adaptations work to maintain cultural identity and coherence. Like species that do not interbreed, human cultures are surprisingly resistant to influences from other cultures and often act as barriers to gene flow. Important elements of culture show dominantly vertical modes of inheritance, much like the vertical transmission of genetic information. Collections of different species are observed to distribute themselves geographically in accordance with clear lawlike patterns, and so, too, do human cultures. At a psychological level, humans display forms of social behaviour conducive to living in small groups, such as rewarding cooperation, punishing those who deviate from norms, and being wary of outsiders.

Cultures and species

But what is culture? This is one of those concepts that resists easy definition, even though most of us know which culture we belong to and who its other members are. We will use a simple definition that links cultures to distinct language groups (Box 1, overleaf), but it almost certainly underestimates their true diversity.

To see how human cultures partition the world like so many species, one need only look to linguistic diversity. Language–culture groups are not evenly distributed. Some 700 to 1,000 different languages, about 15% of the total on Earth, are spoken in the 312,000 square miles of the island of New Guinea⁶. In the northwest coastal areas a different language may be spoken every few miles. Similar densities of languages can be found on many Pacific island archipelagoes. By comparison, about 500 different languages were spoken in all of North America at the time of European contact, and only about 90 are spoken in China despite its vast population and area about 12 times the size of New Guinea. What determines variation in the density (numbers per unit area) of cultures?

One powerful factor is the environment. By 1953, the anthropologist J. B. Birdsell⁷ had documented the greater density of Australian Aboriginal tribal groups in wetter areas, and others have since reported higher cultural densities in coastal and equatorial regions⁸. In animals, a trend called Rapaport's rule⁹ holds that the density of animal species is highest in equatorial regions and declines steadily towards the poles. Polar regions support less biodiversity.

Some years ago, we tested Rapaport's rule in humans using information on Native American tribal groups at the time of European contact¹⁰. For each line of latitude, we recorded the number of languages spoken, and plotted its trend (Fig. 1, overleaf). The number of languages (human cultures) found per unit area is high in the lower latitudes and declines as one moves northwards. At extreme northern latitudes only a handful of different cultures inhabit the entire east-west expanse of northern Canada. An almost identical trend emerges in the diversity of different mammal species with latitude^{11,12}. In both cases the declines in diversity are matched by increasing sizes of

Box 1 Culture and language

A definition of culture has proved elusive, and yet this does not make the concept unusable. Biologists have similar difficulties defining species. The biological-species concept proposes that groups of animals form distinct species when they cannot interbreed successfully. Many apparently distinct species — such as horses and zebras or wolves and dogs — can interbreed. But what makes the concept useful nonetheless is that these species normally do not interbreed if other options are available

In this article we adopt a similarly pragmatic approach to cultures. *Collins English Dictionary*, in line with other sources (see refs 27, 28), defines a culture as "the sum total of a set of shared beliefs, values, practices". Precisely what is shared and what is not will never be easy to document, and, like species, not everyone will operate solely within their culture.

A rough guide to the number of different cultural groups can be obtained by taking them to be synonymous with distinct language groups, for which classification we rely on standard handbooks of the world's languages²⁹. This definition almost certainly underestimates the true number of distinct cultures. **M.P. & R.M.**

geographical ranges. Northerly dwelling animals are found over a large area, and so are northerly dwelling human cultural groups. A single species — humans — carved up North America as might 500 different species of mammal. Studies of African language– culture groups also find that biological and cultural diversity co-vary¹³.

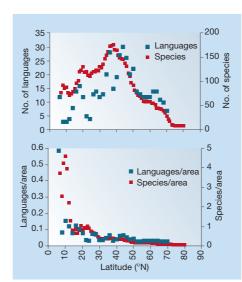
Ecologists explain the trend in species diversity by noting that northern regions experience wider annual variation in climate. This favours species that are ecological generalists, able to cope with a range of conditions. The reverse is true for equatorial regions, where the relative annual stability selects for specialization in a particular habitat or niche. This explanation may be correct for animal species¹¹ but cannot work for humans. Apart from being just a single species, we are unequalled generalists, having colonized virtually the entire Earth through our ability to build fires, make clothes and shelters, and eat a variety of foods.

We believe that a more fundamental tendency accounts for the cultural patterns with latitude. The low cultural diversity seen in northerly latitudes is understandable, even expected. In this relatively unproductive environment, individuals must range over large areas to eke out a living. This movement of people tends to homogenize culture and language. The puzzle is to explain the higher cultural densities in more productive areas. Why do humans not just form one large and homogeneous cultural group in ecologically richer areas such as New Guinea?

It may be that human subpopulations continually split off from larger groups, and form around defensible resources — be they tracts of forest or fishing grounds — because individuals seek to control those resources. Similarities between human cultural and mammalian species diversity may then emerge because the same ecological factors make it more or less likely that small groups can be viable. Over time, these self-sufficient groups emerge as daughter cultures and then as fully fledged different societies with their own customs, specializations and behavioural rules. The speed of cultural evolution makes this plausible. Even a new language can emerge after as few as 500 years of isolation. But we also suggest that it happens because human cultures have evolved mechanisms for maintaining their separation from other cultures.

Cultures and gene flow

For cultural variation to arise in the way we suggest, cultures must act to exclude each other. Anthropologists and linguists can construct family trees of major language groups based on the similarities between the languages. These trees — called phylogenies — chart the genealogical relationships between language groups. Since the late 1980s it has been known that phylogenetic trees of major language groups correspond closely to phylogenetic trees constructed from human genetic markers¹⁴. This result is consistent with our view, yet it may not be surprising: when, owing to



isolation for whatever reasons, people diverge from one another on background genetic markers, their languages and cultures also tend to drift apart.

But studies of European genetic diversity show that language differences may reduce genetic exchange between populations. Robert Sokal^{15,16} and colleagues measured the frequency of 63 genetic markers in samples taken from 3,119 different locations across Europe. They then applied the method of 'wombling' (after W. H. Womble¹⁷) to measure the rate of change in gene frequencies between these different locations. Standard genetic theory tells us that if people diffuse over an area such as Europe, then no boundaries of abrupt genetic difference are expected. However, barriers to the movement of people can produce zones of abrupt change.

Sokal et al. identified 33 boundaries separating areas of especially sharp changes in gene frequencies across Europe, and drew them on a map (Fig. 2). Twenty-two of the boundaries correspond to physical boundaries such as the Alps or the English Channel. They are also linguistic boundaries. For a further 11 boundaries, no physical or other barrier could be detected, and yet nine of these correspond to linguistic boundaries. In all, then, language is associated with regions of abrupt genetic change in 31 of the 33 cases. Not all studies support the separation of genes and language¹⁸, but it does seem that humans are more likely to mate with people they can talk to! The consequence is that cultural differences become self-reinforcing, prompting further cultural divergence.

Cultural transmission

Cultures also separate themselves from other cultures by the ways in which they transmit cultural information. Conventionally, we can describe vertical and horizontal modes of transmission of both genetic and cultural traits. The dominant mode of

Figure 1 Language, mammals and Rapaport's rule. Top, Numbers of languages and of mammal species at each degree of north latitude in North America. The trends reflect the shape of the continent, being narrow in the south regions and growing wider at higher latitudes. Both trends peak at about 40° N, where North America is about 3,000 miles wide. (Data from refs 10 and 11.) Bottom, Densities of languages and mammal species, calculated as the number of either at a given latitude divided by the area of the continent for a 1° latitudinal slice at each latitude. Having controlled for area, both trends show the decline in density characteristic of Rapaport's rule⁹. Similar latitudinal trends for language and species diversity have been reported for Africa¹³.

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transmission for both kinds of trait is vertical: parents transmit genes to offspring, and cultural traits are transmitted down generations by parents, elders and teachers. Nearly all of us speak our parents' language, and political and religious beliefs are surprisingly stable over generations. Humans are especially likely to copy common traits, a tendency that works to reduce variation within a culture but increase it between cultures. Genetic information is also sometimes transmitted horizontally, such as when a virus or other vector carries genetic material from one species to another. Normally, however, species barriers to interbreeding prevent large-scale horizontal transfer of genetic information, and it is an oddity when it is observed. We share more than 98% of our genes with chimpanzees because our genome is largely a closed shop to other genomes.

Barriers to horizontal transmission of culture are, in principle, far weaker. Horizontal transmission may sometimes be imposed, as when one culture conquers another. More prosaically, however, cultural traits can diffuse among geographically close neighbours, as when one culture borrows or adopts words, ideas, customs and technologies from another. The English language is an example, with about half of its vocabulary being of Germanic origin (vertical transmission) and half of Romance origin, reflecting, among other forces, the Norman conquest of England in the eleventh century. Of course, cultures do not always survive contact with one another, because a politically, technologically or economically dominant culture frequently displaces a weaker one.

It is revealing for our argument to consider how cultures treat events of horizontal transmission. Whereas vertical transmission of cultural traits goes largely unnoticed, horizontal transmission is far more likely to be regarded with suspicion or even indignation. France, for example, devotes a ministry to slowing or banning what is portrayed as an overwhelming march of English words, customs and phrases into the French language and culture. While the other nations of the world work away on their computers, the French sit at their ordinateur. The British are similarly alert to what they perceive to be 'Americanisms'. In both cases the home population is seen as an unwilling victim. However, a recent study of the English language found that it had admitted at least 90,000 new meanings over the past century, with only 5% derived from borrowings¹⁹. If there is an enemy, it is within. Cultures, it seems, like to shoot messengers.

These anecdotal accounts can be placed upon a firmer footing. If horizontal transmission is strong, cultures should tend to share their traits with those of their nearest geographical neighbours. If vertical transmission predominates, cultures

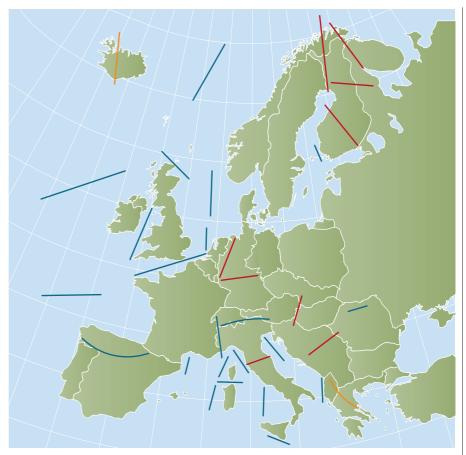


Figure 2 Genes and language in Europe. This map shows lines that divide regions of abrupt differences in the frequencies of 63 genetic markers in Europe's populations. The 22 blue lines identify regions that are separated by both physical barriers, such as the Alps or the English Channel, and linguistic differences. The 11 red and orange lines divide regions that have no detectable physical barriers, yet nine of the 11 (those in red) correspond to linguistic differences. In this case, then, language is associated with abrupt genetic change in 31 of 33 cases. Some lines fall in the sea (such as between Ireland and Iceland), indicating that the theoretical point of rapid genetic difference falls somewhere between the two locales and not on either one of them. (Map, redrawn from ref. 16, shows Europe of 1990, and provides a detailed key to the linguistic and other boundaries corresponding to the lines.)

should tend to have the traits of the cultures from which they descend; that is, of their ancestral culture (Box 2, overleaf). Although geography and ancestry are often correlated, a statistic known as the Mantel test²⁰ can distinguish the two hypotheses. In a study of 47 cultural traits in 277 African societies, most traits examined, especially those affecting means of subsistence, family structure and kinship (traits closely associated with reproductive success), were conserved over generations²¹. The only traits to show clustering that was dominantly geographical pertained to sexual division of labour. Another investigation, using a worldwide sample of cultures, found that subsistence practices, mating systems and sexual division of labour flowed down generations²². These results are striking: even under the influence of close geographical neighbours, cultures can remain stable and coherent units. Borrowing and imitation certainly occur. But cultural evolution is not a freefor-all in which all traits become equally available for adoption each generation.

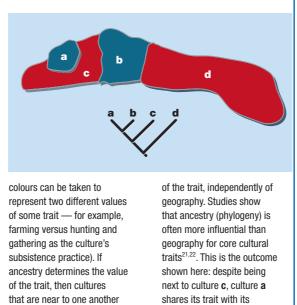
Extreme sociality

Human cultures are not as impermeable to outside influences as genomes, but they do erect barriers to the movement of people and ideas. What is so valuable as to call for this much protection? In a word, the answer is the group itself. It seems likely that human evolution in general, and human cultural evolution in particular, is distinguished by its sophisticated group behaviour. Historically, groups have had cooperative jobs to do, such as hunting large prey or warring with other human groups for access to territory or mates. These jobs are too large for any one person, placing a premium on group coherence, communication and cooperation.

The trouble is that this also makes cheating more profitable. The evolutionary theorist William Hamilton²³ argued that, to protect themselves, cooperative groups evolve strategies to make admission into their ranks difficult. These can take the form of being wary of outsiders, long periods of probation and costly (to the initiate)

Box 2 Transmission of cultural traits

The ancestor-descendant relationships between a group of cultures can be represented by a phylogenetic tree. Phylogenies are branching diagrams, like a genealogy or a family tree, that describe relatedness between a group of species or cultures. Linguistic data can be used to construct phylogenies of cultures for comparative cross-cultural studies^{30,31} in much the same way that genetic data can be used to construct phylogenies of animals. The diagram shows a hypothetical geographical area with four cultures labelled **a–d**. If geography determines the traits that any two cultures have in common, then, for example, cultures a and c should share the trait (the two



on the phylogenetic tree

should have the same value

initiation ceremonies. This works to a degree, but cheats can still arise from within the group. Theorizing about group behaviour has therefore also emphasized the importance of genetic relatedness between group members. When it is high (as can be achieved if immigration is kept at a low level), altruistic and cooperative behaviours flourish because they tend to benefit one's own relatives. But genetic relatedness has its limitations. When it gets too high within a group, inbreeding begins to take its toll, and the benefits of sexual reproduction, namely the mixing and recombining of genes, are diminished.

Humans may have worked out a way to discard the need for relatedness as a means of ensuring cooperation: uniquely among the animals, humans may carry a set of behavioural adaptations specific to promoting cooperation and reciprocity, even when relatedness is low between group members^{24,25}. According to the doctrine known as strong reciprocity, humans are predisposed to cooperate with others, to make fair distribution of gains, and to punish those who fail to cooperate, even at a cost to themselves and with no expectation that these costs will be repaid^{24,25}.

This is a remarkable assertion, but should we believe it? Theoretical studies show that norms of cooperation and punishment of cheats can arise and be maintained in groups by a process of cultural 'group selection', in which more cohesive and cooperative groups outcompete groups riven by selfish cheats. Over time, these kinds of cooperative groups come to dominate. Laboratory experiments with volunteers and cross-cultural studies seem to support the strong-reciprocity view. There are implicit norms of cooperation in groups, and individuals seem willing to punish cheats altruistically — that is, the punisher pays the cost of punishing — even though all group members reap the benefits.

relative.

nearest phylogenetic

M.P. & R.M.

This extreme sociality can make cooperation a stable strategy resistant to cheating even when group members are not related. But it does depend upon one key demographic feature: migration between groups must be kept low. If it is not, groups become homogenized, cheats can prosper and the driving force of group selection — differences between groups — fails. Wariness of strangers, for all its potentially ugly manifestations, may be deep in our psychological make-up.

An unscientific postscript

We end by taking our cue from the existential philosopher Søren Kierkegaard²⁶. If the view put forward here is correct, then human cultural diversity arises from two main forces. One is the drive to secede from larger groups whenever possible, the better to control some defensible resource; this is what gives rise to the geographical patterns of diversity. The second set of forces is social and behavioural. They maintain cooperation within groups and create cultural identity and coherence, causing barriers to gene flow and meaning that vertical cultural transmission dominates.

Putting these forces together, we get a picture of humans as a highly social and group-focused species. None of this is to say that selfish behaviour has been erased or that all cultures survive intact. The all-toocommon 'tragedies of the commons', in which individual over-exploitation of common resources results in their collapse, remind us of the price of selfishness. But this picture of the nature of cultures suggests that they are surprisingly robust against outside influences (although not invincible) and that, at least for large cultures, worries about cultural swamping are overstated. Nevertheless, our ancient cultural practices may also be telling us that, in a world in which mass movements of people from poorer to richer areas will become ever more common, we must be especially vigilant about our own tendencies to protect the status quo ante.

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1. Harris, M. Cows, Pigs, Wars and Witches: The Riddles of Culture (Vintage, New York, reissue edn, 1989).

- Renfrew, C. Archaeology and Language: The Puzzle of Indo-European Origins (Penguin, London, 1987).
- 3. Diamond, J. & Bellwood, P. Science 300, 597-603 (2003).
- Kaessmann, H., Wiebe, V. & Pääbo, S. Science 286, 1159–1162 (1999).
- Kaessmann, H., Heissig, F., von Haeseler, A. & Pääbo, S. Nature Genet. 22, 78 (1999).
- Wurm, S. in Atlas of the World's Languages (eds Moseley, C. & Asher, R. E.) 93–158 (Routledge, London, 1994).
- 7. Birdsell, J. B. Am. Nat. 87, 171–207 (1953).
- 8. Nichols, J. Evol. Anthropol. 3, 206–215 (1995).
- 9. Rapaport, E. H. Science 201, 679–686 (1982).
- 10. Mace, R. & Pagel, M. Proc. R. Soc. Lond. B 261, 117-121 (1995).
- Pagel, M. D., May, R. M. & Collie, A. Am. Nat. 137, 791–815 (1991).
 Pagel, M. in The Evolutionary Emergence of Language
- (eds Knight, C., Studdert-Kennedy, M. & Hurford, J.) 391–416 (Cambridge Univ. Press, 2000).
- Moore, J. L. et al. Proc. R. Soc. Lond. B 269, 1645–1653 (2002).
 Cavalli-Sforza, L. L., Piazza, A., Menozzi, P. & Mountain, J.
- Proc. Natl Acad. Sci. USA 85, 6002–6006 (1988).
 15. Sokal, R. R. et al. Am. Nat. 135, 157–175 (1990).
- Barbujani, G. & Sokal, R. R. Proc. Natl Acad. Sci. USA 87, 1816–1819 (1990).
- 17. Womble, W. H. Science 114, 315-322 (1951).
- 18. Rosser, Z. H. et al. Am. J. Hum. Genet. 67, 1526–1543 (2000).
- 19. Dent, S. The Language Report (Oxford Univ. Press, 2003).
- 20. Mantel, N. Cancer Res. 27, 209-220 (1967).
- Guglielmino, C. R., Viganotti, C., Hewlett, B. & Cavalli-Sforza, L. L. Proc. Natl Acad. Sci. USA 92, 7585–7589 (1995).
- Holden, C. & Mace, R. Am. J. Phys. Anthropol. 10, 27–45 (1999).
 Hamilton, W. H. in ASA Studies 4: Biosocial Anthropology (ed. Fox, R.) 133–153 (Malaby, London, 1975).
- You, K. J. 153–153 (Mataby, Euhadin, 1973).
 Fehr, E. & Fischbacher, U. *Nature* 425, 785–791 (2003).
 Gintis, H., Bowles, S., Boyd, R. & Fehr, E. *Evol. Hum. Behav.* 24,
- 153–172 (2003). 26. Kierkegaard, S. Concluding Unscientific PostScript to
- Philosophical Fragments, 1846 (transl. Hong, H. V. & Hong, E. H.; Princeton Univ. Press, 1992).
- Durham, W. H. Coevolution: Genes, Culture and Human Diversity (Stanford Univ. Press, 1991).
- Cavalli-Sforza, L. L. & Feldman, M. W. Cultural Transmission and Evolution: A Quantitative Approach (Princeton Univ. Press, 1981).
- Ruhlen, M. A Guide to the World's Languages Vol. 1 Classification (Arnold, London, 1991).
- 30. Mace, R. & Pagel, M. Curr. Anthropol. **35**, 549–564 (1994). 31. Pagel, M. in *Time–Depth in Historical Linguistics*
- (eds Renfrew, C., MacMahon, A. & Trask, L.) 189–207 (McDonald Inst. Archaeology, Cambridge, 2000).
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