Human phylogeography and diversity

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Homo sapiens phylogeography begins with the species' origin nearly 200 kya in Africa. First signs of the species outside Africa (in Arabia) are from 125 kya. Earliest dates elsewhere are now 100 kya in China, 45 kya in Australia and southern Europe (maybe even 60 kya in Australia), 32 kya in northeast Siberia, and maybe 20 kya in the Americas. Humans reached arctic regions and oceanic islands last—arctic North America about 5 kya, mid- and eastern Pacific islands about 2–1 kya, and New Zealand about 700 y ago. Initial routes along coasts seem the most likely given abundant and easily harvested shellfish there as indicated by huge ancient oyster shell middens on all continents. Nevertheless, the effect of geographic barriers—mountains and oceans—is clear. The phylogeographic pattern of diasporas from several single origins—northeast Africa to Eurasia, southeast Eurasia to Australia, and northeast Siberia to the Americas—allows the equivalent of a repeat experiment on the relation between geography and phylogenetic and cultural diversity. On all continents, cultural diversity is high in productive low latitudes, presumably because such regions can support populations of sustainable size in a small area, therefore allowing a high density of cultures. Of course, other factors operate. South America has an unusually low density of cultures in its tropical latitudes. A likely factor is the phylogeographic movement of peoples from the Old World bringing novel and hence, lethal diseases to the New World, a foretaste, perhaps, of present day global transport of tropical diseases.

biogeography | diversity | diaspora | Old World | New World

Human phylogeography has been for decades and is still studied under the rubric of physical anthropology or biological anthropology. Among other interests, these fields investigate the global spread of hominids, hominins, and humans. In doing so, they use all methods and sources of information available. The two fields and hence, the discipline of human phylogeography also investigate the many correlates of our species' distribution across the varied environments of the world—physiology, genetics, behavior, anatomy, commensals, and also, a special form of behavior, namely culture. Here, within the topic of human phylogeography, I address the geographic spread of the human species across the world and the influence of the environment on regional cultural diversity.

In both the professional and popular literature, the word "human" sometimes refers to all *Homo* species or even the non-*Homo* genus, *Australopithecus*. I use the word to mean only *Homo sapiens*.

Human Species' Global Diaspora

African Origins. The earliest signs so far of humans, *H. sapiens*, are cranial fragments in southwest Ethiopia with a suggested date of 195 kya (1). (All ages are in calendar years ago and not isotope years ago.) However, the range of possible dates of the fragments is, in fact, 195–105 kya. The next oldest remains are from around 165 kya, also in Ethiopia (2). Preceding *H. sapiens*, several other *Homo* species and their ancestors, *Australopithecus* species, were African too (ref. 3, chap. 5).

This summary hides considerable debate about nearly all aspects of human origins, even whether our species had a single origin (ref. 3, chap. 5). Not only that but also, new finds continually change our understanding, especially in a continent as little investigated as Africa. Whether, then, the human species arose in Ethiopia or arrived there from elsewhere in Africa is still an open question (4, 5).

Be that as it may, by 100 kya, humans lived over much of Africa (ref. 3, chap. 5). Indeed, humans had left Africa by then. Stone tools along with the bones of humans who made them that date to about 125 kya have been found in southeast Arabia (6). Until recently, both archeological and anatomical evidence indicated that humans got no farther until about 60 kya (7, 8) or maybe a little over 70 kya (9). It seemed that the aridity of an approaching ice age might have prevented farther expansion or indeed, led to the disappearance of humans from the Arabian Peninsula.

However, increasingly older dates east of Arabia indicate the need for rethinking of at least the dating of our diaspora out of Africa. For instance, a date of about 45 kya for humans' arrival in Australia (10) might need to be extended to 60 kya (11). Other dates elsewhere are perhaps too recently published to be independently tested (for instance, the date of 67 kya from a single metatarsal of a potential human in the Philippines) (12). Another in southern India at 74 kya is already disputed. The date comes from volcanic ash around microlithic artifacts (13). However, no bones are associated with the artifacts, and humans might not even have made them (14). Given the nature of the tools, the next likeliest toolmaker is Neanderthal, but the nearest Neanderthal remains are over 2,000 km away.

If some more distant dates might be wrong, dates almost always get older. In 2015, excavations in southern China revealed "unequivocal" human teeth dated to 120–80 kya (15). A previous similarly aged find for that region is disputed (9), but if the recent find and claim is substantiated and especially, if the older end of the range of dates is substantiated, it becomes possible that, in fact, the first exodus from Africa continued on east.

The last interglacial period was at its height 125 kya. The climate and hence, distribution of vegetation were much the same as now. In other words, the environment was favorable by comparison with the Old World aridity of a glacial period. The Sahara might have been in some regions wooded savannah and hence, good habitat then for migrating humans (16, 17). By 60 kya, however, the approaching ice age should have been associated with a drying climate in Africa, which leads to the suggestion that aridity drove the African exodus (18).

However, Lake Malawi sediments indicate a warm and wet eastern Africa at about 75 kya (19). Far from poor conditions driving dispersal, maybe good conditions and an increasing human population did so. Currently, we do not have enough information on African paleoclimates or the trajectory of African populations to distinguish these two scenarios (refs. 20, chap. 3 and 21).

Assuming no advanced rafting capabilities, the early dispersers from Africa must have entered the Arabian Peninsula across the marshes at the north end of the Red Sea, perhaps properly the Reed Sea (22). By whatever route they arrived on the eastern coast of the Arabian Peninsula, a northern dry-shod route round the north end of the Persian Gulf then seems likely.

However, at 60 kya, the Red Sea's narrowest point at the southern end might have been less than 20 km across. Ethiopians there could have seen Arabia across the Bab el Mandeb Strait. After they arrived in southeast Arabia, the dispersing humans would have found the Strait of Hormuz between them and Iran to have been only about 50 km across. Because maybe only 15,000 y later, at 45 kya, humans had reached Australia across 100 km of ocean (whether they arrived through Indonesia or New Guinea), maybe a southern route into Arabia and then, Iran is not impossible (9). Indeed, modeling that took into account parameters, such as lowered sea levels, climate, the nature of the environment, and a preference for coastal travel, suggests one or both southern crossings as possible, even likely (23, 24).

The dates given so far and the evidence for Africa as the phylogeographic origin of the human species come largely from archeology and paleontology. Genetics confirm humans' African origin. A recent origin from a single small population is indicated by the fact that the human species is less genetically diverse than some populations of chimpanzees (25, 26). The size of the world's founding diaspora out of Africa is debatable, but genetic analyses indicate a figure of a few hundred (27). Humans' geographic origin in Africa is indicated by the fact that human molecular diversity is greatest in Africa (28, 29). For instance, although four main mtDNA forms exist in African populations, only two exist outside, both from just one of the African forms (30, 31). Also, people of almost any region in the world are more genetically different from African populations than they are from all other populations (ref. 32, chap. 2). Such lines of evidence of humans' African origin have been repeatedly confirmed, including with morphological analyses (33, 34).

Humans arriving in Eurasia from Africa could have met Neanderthals and even Denisovans. Indeed, some genetic analyses indicate that humans mated with both of these other hominins (35–38). The findings are disputed, however, with the suggestion that, instead or in part, they could indicate descent from a common ancestor, the population of which was structured (i.e., genetically heterogeneous geographically), which realistically will almost always be the case over any appreciable area (39).

Old World Outside Africa. The oldest, largely accepted dates of humans outside of Arabia all fall around 50–40 kya regardless of whether in Asia, Australia, or Europe (10, 11, 40–43). However, as already indicated, not only have several studies suggested older dates, but the chances of finding the oldest evidence are so slim that oldest dates must inevitably get older.

New Guinea, Australia, and Tasmania at 50 kya were a single continent, Sahul. One geographic source for the peopling of both New Guinea and Australia is, thus, a possibility (indeed, on genetic grounds, perhaps a likelihood) (9). Nevertheless, a separate migration into each is also possible (44, 45). The shortest sea crossings in either case would have been, to repeat, about 100 km.

Subsequent to the earliest arrivals in New Guinea and Australia, these two populations could have remained separate from each other and the rest of the Old World for the next 40,000 y (46). In New Guinea, a significant late introduction was that of the sweet potato a little over 300 y ago, which allowed expansion of agriculture and hence, populations to regions too high or poor for the previous main food crop, taro (47).

By around 5 kya, the Pama–Nyungan language family originating in northeast Australia covered most of Australia, except the far northwest and the continent's dry interior (48, 49). The Pama–Nyungan-speaking peoples entered the latter in the first millennium AD, about 3,000 y after Australia's 40,000 y isolation ended with an immigration that brought the dingo with it, probably from India (50).

Tasmania was part of Sahul until around 8 kya, when rising seas finally formed the Bass Strait. Despite no sea barrier between Tasmania and Australia before that, Tasmania's first inhabitants apparently arrived only 35 kya, 10,000 y after first confirmed arrival in Australia (51).

The deliberate near eradication two centuries ago of native Tasmanians by arriving Europeans, largely British, means a paucity of genetic or linguistic information from which to judge origins, migrations, and settlement in the region. Nevertheless, linguists have identified five main groupings apparently so different from one another that the only words in common are largely those applying to European introductions, for example, of livestock (52).

In Europe itself, the earliest dates in the west are for sites in the heel of Italy at around 44 kya (53), and about 43 kya in southern Britain (54). In other words, people were moving north as the peak of the ice age was rapidly approaching. However, the drop in temperature in the northern hemisphere from the peak interglacial at about 125 kya to the peak ice age at around 25 kya was erratic. Several times temperatures rose to nearly match the interglacial maximum, including at about 45 kya (9).

At the height of the ice age, however, the European ice cap covered Scandinavia and northern Europe down to northern Germany and the middle of Britain and Ireland. Evidence so far indicates that humans retreated from almost all of northern Europe. They returned to Britain from the Basque region of northern Spain about 10 kya (55) or around 1,000 y after the beginning of the Neolithic revolution and the expansion of agriculture into Europe from the Near East (56). Celts and then Anglo-Saxons followed in historical times from mainland western Europe (57).

The words Basque, Celt, and Anglo-Saxon that I have just used describe both cultures and peoples, as with descriptors of cultures and peoples all over the world. In theory, a culture could move independently of its originating population. In practice, cultures usually move only because people move (32, 58). This coordinated movement is a specific example of a general pattern (59). In jargon, cultures are transmitted vertically and not horizontally. However, exceptions exist. Of 19 skeletons at a burial site in Oxford, England, the isotope ratios in the teeth of 18 of the people were the same as in the local soil. In other words, they were native-born. However, the burial site was culturally Anglo-Saxon (60). In this case, the residents had adopted the culture of the invaders.

Four thousand years before humans were in Italy, they were on the central north coast of Siberia at Yenisei Bay hundreds of kilometers above the Arctic Circle. We know this from clear signs of killing and dismemberment of a mammoth and dating of the find (57). Sources differ on whether the region was eventually covered by the northern ice cap. However, farther to the east, at the famous Yana Rhinoceros Horn site in far northeast Siberia, the humans there at 32 kya (61) could have remained through the ice age, because the climate in eastern Siberia was too dry to support an ice sheet.

Genetic evidence indicates that people in northeastern Siberia arrived there from south central Russia (62), although some linguistic evidence indicates north central Russia also (63). A recent surprise is evidence from a 24-kya site near Lake Baikal in central south Siberia of a large genetic component of western European origin (64). The same genetic signature was detected at a 17-kya site 600 km northwest of the Lake Baikal site, implying that people remained in at least southern Siberia through the peak of the last ice age (64).

The earliest signs so far of humans elsewhere in eastern Asia are from around 40 kya, although a genetic analysis indicates 60 kya for eastern Asia and a little under 40 kya for Japan (65). Humans in Hokkaido, the northernmost island of Japan, could be from southeast Siberia, but those in the southern islands are from Korea (66). That double phylogeographic origin is the pattern also for Japan's other mammals. Within Japan, the two geographic origins are indicated by the so-called Blakiston's Line through the Tsuguru Strait between Hokkaido and Honshu. With the approaching ice age's lowering of sea levels, the original human immigrants could have arrived overland. However, movements to outlying islands from maybe 9 kya were over sea. Japan experienced several

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subsequent immigrations, with one at nearly 3 kya producing perhaps the largest genetic contribution to the islands (67, 68).

Elsewhere in Asia, topography as well as cold might have been a barrier to movement, because the earliest signs of humans in Tibet date to 31 kya (69). The Himalayas as a barrier is nicely shown by the greater genetic distance between people on either side of them than the average for the same geographic distance elsewhere (70).

Movement Within and into Africa. Of course, as humans spread across the Old World outside of Africa, they also spread within Africa. For instance, Y-chromosome analyses indicate links of west and east African pygmoid peoples with the ancient southern African Khoisan/San peoples (71) and between west African pygmoid peoples and east African Hadza peoples (72). Although the field of phylogeography usually uses genetics as its evidence, genetics need not be its only tool. Corresponding to genetic indications of links between eastern and southern African peoples, the rock art of Ituri pygmoid peoples in eastern Zaire is apparently similar to that of Khoi peoples in southern Africa (72) (Khoisan, Khoi, San, Khoe, and Khoenkhoen are sometimes distinguished in the literature and sometimes not). One of the latest and largest movements within Africa was the expansion of the Bantu peoples from around maybe 3 kya judged from archeology, genetics, and linguistics (73, 74).

In historic times, the slave trade produced probably the fastest movement of large numbers of Africans from sub-Saharan Africa into North Africa. People also moved back into Africa from the rest of the Old World (5, 75) [hence, for example, the surprising finding that the San Khomani peoples of South Africa, outwardly similar to the adjacent San Namibia, have about 10% admixture of western European genes (76)].

Americas. Until the last ice age, the Bering Strait was a barrier between the Old and New Worlds. However, although 80 km across now, the strait was a broad flat expanse of land about 50 m above sea level during the peak of the ice age. Then or later, Siberians crossed into Alaska.

An allele and a single blood group, both almost ubiquitous among Native American and Amerindian populations and both present in eastern Siberians, indicate that a very small population from Siberia peopled the New World (32, 77). For instance, although northeastern Siberians have all three major blood groups (A, B, and O), more than 95% of native Amerindians are O (32). As said, the northeastern Siberians are, in part, genetically western European. That being the case and given that Native Americans of both Americas originated in northeast Siberia, then western European genes in Native Americans is perhaps inevitable. The extent of contribution might be surprising, however. One calculation has the western European complement constituting perhaps one-quarter of the Native American genome (64).

As elsewhere in the world, these earliest arrivals could well have traveled first down the coast of both continents (78, 79). Regarding timing of their entry into the Americas, previously accepted estimates of earliest arrivals now need revision. The quite widely accepted earliest date for the presence of humans in North America was 15.5 kya for a site in central Texas (80). South America's earliest date was 14.5 kya from the famous Monte Verde site in southern Chile (81, 82). However, those finds are now superseded by a 2015 report of at least 18 kya at Monte Verde (83) and a 2014 report of dates of roughly 30–20 kya in northeast Brazil (84). This latter finding makes a formerly largely rejected claim of around 32 kya in northeast Brazil (85) now not so incredible.

These dates in both Americas along with several others before them must silence all future mention of the "Clovis-first" hypothesis, namely that the people of the Clovis culture were the first into North America at about 13 kya. Nevertheless, the Clovis people and their culture were phylogeographically successful. The genotype of an infant from 12.6 kya found in western Montana

tightly associated with Clovis tools indicates not only a strong Siberian heritage but also, a strong genetic link to most Native North American peoples as if Clovis replaced the previous North Americans (86). Either the prior immigrants stuck to the coast, not moving inland, or before they could densely populate North America, the Clovis peoples entered and superseded them.

Monte Verde in southern Chile is about 16,000 km from Siberia. How long it took these first Americans to reach southern South America, we have little to no idea, given that the oldest South American dates are now older than the oldest North American dates. One line of evidence could be the distances traveled by relatively modern nonsedentary traditional societies. In the Americas, they moved camp a median of about 100 km/y (87). At that rate and with straight line travel down the coast, humans would have taken less than two centuries to travel from Alaska to Monte Verde.

Alternatively, humans moved through the world by demographic expansion. Moving into continents empty of humans and moving into prey populations unused to humans and hence, easily hunted, the expansion could have been rapid. A calculation that accounted for number and distance of camp movements, frequency of foraging forays, reproductive rates, rate of population increase, costs of carrying children, hunting and foraging returns, and potential for children to contribute to the diet concluded that the 16,000-km journey in 2,000 y was possible even with a high rate of reproduction and hence, the necessity to feed and carry children (88). After all, that time for that distance translates to less than 25 m/d.

A main reason why fast movement could be compatible with high rates of reproduction was that women at the vanguard of the advance into virgin territory might have needed to forage just one-quarter of the distance of those following behind and entering depleted land. Indeed, across hunter–gatherer societies, those with more camp moves per year can reproduce more than those with fewer (88).

Similarly, an analysis of eastern Canadian genealogies indicated that the ancestors of the current population who were at the front of the population expanding through the region in the 300 y to the mid-1900s contributed more to the present day gene pool than did people from the core of the population's range (89). An explanation for the phenomenon comes from the genealogies of females in the region, which indicate that those at the front had 15% more offspring than those behind and 20% more married children (89).

We know little about original human movement through the Amazon, in part because archeology across large expanses of forest is difficult. Not only that but Amazonia might have lost nearly two-thirds of its languages as a result of European invasion (90). The same is true of the Caribbean. Earliest archeological remains in that region are in Cuba from about 7 kya and might be associated with a chert quarrying industry tied to Belize (91). The next signs of movement into the Caribbean, judged by archeology, are immigrations from the north of South America about 2.5 kya, and they continue from then (91).

By about 12.5 kya, humans were in the high Andes: at over 3,000 m in Chile and Argentina and over 4,000 m in Peru (92). These high-altitude dates are several thousand years after humans arrived in coastal South America. The dates come from the collagen of large bones of camelids directly associated with stone tool workshop sites. The significance of large bones is that they are less likely to have sunk to layers lower than those in which they first fell.

Later, in the middle of the last millennium, the Incas provide an example of colonization by migration of people as opposed to slow demographic expansion. Within a century, they conquered a multiethnic region 4,000-km long controlled with over 20,000 km of paths and roads, most of them paved (93). Furthermore, the control apparently involved relocation of entire native communities for both economic and defense purposes. A little later, the Spanish did the same, moving tens of thousands to work in and around the Bolivian silver mines (93).

Six hundred years before the Spanish arrival, the Wari of Peru were trading products from nearly 1,000 km away (93). The huge

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cities then and later—a Wari one of about 15 km², for example—also indicate great movements of peoples, forced or voluntary, into main centers of production, just as happens today (94).

Movement east from eastern Beringia into the north of North America had to wait for the near disappearance of the northern ice cap, which extended south to Washington in the west and New York in the east. That movement seemingly did not happen until about 5 kya, with the diaspora of the Eskimo–Aleut peoples from first Siberia and then, Alaska across to Newfoundland and west coast Greenland, while the Inuit occupied Alaska (95–97).

Oceans. By the time that humans had reached northern Siberia 32 kya, they were beginning to move across the Pacific north and east of New Guinea. They had reached the Bismarck Archipelago by then, east of New Guinea (98). Assuming island hopping along the way, the longest sea crossing would have been about 75 km.

Not until maybe 4,000 y ago did they get any farther. Then, they rapidly expanded across the western Pacific, north into Micronesia, and southeast as far as Fiji in southeastern Melanesia by about 3,200 y ago (99–101). Fiji is about 1,000 km east of New Caledonia and 800 km east of New Hebrides. Large oceangoing sea crafts were necessary for such a voyage.

As in the Americas, an unexploited fauna and flora could well have allowed the rapid expansion, perhaps especially a fauna unused to being hunted (in the case of many birds, flightless). Archeologically, this expansion is indicated by finely decorated Lapita pottery (102). The name comes from the site in New Caledonia halfway between Australia and Fiji, where it was first identified.

A little under 2,000 y ago, humans reached Tahiti and then, Hawaii by maybe 1,500 y ago or maybe even as late as 800 y ago (99). They got to New Zealand 750 y ago from the Cook Islands 2,500 km to the northeast (31, 99). Given the length of the voyage to New Zealand, a figure of only about 70 founding females (103) might not be surprising but even so, implies several successful crossings along with the degree of variation in mtDNA in the teeth and bones of probable founding individuals (104).

Taiwan seems to be a main origin of the dispersal across the Pacific given that it is the current center of origin of 9 of 10 of the main Austronesian (essentially western and island Pacific) languages (105, 106). Archeology substantiates that view (107). Genetically, a plausible scenario is movement of peoples from Taiwan to eastern Indonesia, perhaps through the Philippines, and thence out into the Pacific. However, the story is complex, with, for instance, different Asian origins for different areas of the Pacific (108) and some contrasting results from Y-chromosome and mtDNA analyses (45, 101, 108).

At about the same time as humans were moving across the last stretches of the Pacific, they were crossing the Indian Ocean. The first successful settlers in Madagascar might have arrived 2,000 y ago (109), even if the first signs of presence are from 3,400 y ago (110). Genetic studies indicate equal contributions to the Malagasy gene pool from Africa and Indonesia (111–113). Even so, the number of Indonesian founding females in Madagascar might have been one-half the number of female founders of New Zealand: about 30 instead of 70 (111).

The Indonesian contribution to the origins of the people of Madagascar is strongly supported by the fact that the language of Madagascar, Malagasy, is mainly Bornean (indeed, from the Barito region of southern Borneo). However, not only were the Barito peoples seafarers, but also, Malagasy has several other Indonesian sources as well as some Malaysian roots as if the original contingent of immigrants boarded from a variety of the islands west of Borneo (114). The most likely route is not directly across the Indian Ocean but coastal and probably by coastal trading (115).

Modern Migrations and Their Barriers. Movements of genes and peoples continue to this day, of course, in response to repression and opportunity. China, for instance, has seen massive migrations.

Some have been organized by the Chinese government; others, especially in the surrounding regions, have occurred in response to events in the regions (116). These movements include migrations of tens of thousands into the cities. Indeed, as already indicated, large flourishing cities are some of the most ethnically dense regions, at least in the United States (117).

Despite such movements, geographic and cultural barriers operate now as in the past. The barriers exist even in western Europe, with its dense transport network (118, 119). Populations either side of mountains or waters are genetically distinct. Indeed, culture itself or language itself is often a barrier because of both difficulty of communication and also, to coin a word, "xenantipathy" or dislike of strangers (120). Thus, a map of the distribution of genotypes across Europe is almost identical to the geographic map of Europe (118). Similarly, across a sample of the Solomon Islands of the Pacific, insular differences in peoples' anatomy correlated more strongly with linguistic differences between the islands than with geographic distance between them (121).

Sex-Specific Phylogeography. So far, I have written as if everything phylogeographic that one of the human sexes did, so also did the other. That uniformity is not necessarily the case.

The Mayflower, one of the first ships from Europe to bring future residents to the future United States, apparently carried three times as many men as women (122). Among migrants and traders, that ratio is usual, with the result that Y-chromosome genotypes are sometimes more widely spread than mtDNA genotypes (123). The result is evident in the Pacific, for example (124), and in the widespread presence of Mongol Y-chromosome genes through Asia and eastern Europe, the legacy of the Khan invasions of the 13th and 14th centuries CE (125).

However, among agriculturalists, males are usually the landowners and hence, tend to be the resident sex, whereas females move in marriage. The result is regional differentiation in Y-chromosome genotypes but regional ubiquity of mtDNA genotypes (126). Furthermore, because a language of a people tends to be that of the invading dominant sex, male, a frequent outcome is a match between regional differentiation in language and Y-chromosome genotype but a mismatch between language and mtDNA genotypes (126).

Iceland epitomizes the contrast (119, 127). All Icelanders speak Icelandic, which is essentially Scandinavian (indeed, originally Norwegian). Scandinavia, especially Norway, is also the genetic origin of the people of eastern Iceland and the males of western Iceland. However, western Iceland's mtDNA profile (i.e., female genetic profile) is quite largely of Gaelic British origin. The first millennium's Viking raids into western Britain and the abduction of women from there to western Iceland would explain that pattern.

Phylogeography of Human Commensals. I have so far indicated how archeology, genetics, and linguistics elucidate human phylogeography and in so doing, indicated how genetics and culture can determine human phylogeographic patterns. Human phylogeography uses an additional source of information—the phylogeography of the organisms that live with us, on us, and in us.

The global phylogeography of several organisms responsible for human disease and infection matches that of their human hosts (128). For instance, the human malaria organism, *Plasmodium falciparum*, is most genetically diverse in Africa, loses genetic diversity the farther that it is from Africa, loses similarity to African *P. falciparum* the farther it is from Africa, and probably left Africa 60–50 kya (129). The same pattern occurs in *Helicobacter pylori*, the human stomach bacterium (130). Its phylogeography not only maps onto human immigration into the Americas more than 12 kya but also, maps onto the Neolithic introduction of farming into Europe, the Bantu expansion within Africa, European immigration into the Americas, and the slave trade from Africa into the Americas (130) as well as onto the spread of humans across the Pacific (131).

The diaspora across the Pacific of the paper mulberry *Broussonetia papyrifera*, a lizard *Lipinia noctua*, pigs, and the Pacific rat *Rattus exulans* as judged genetically must also be a result of the diaspora of humans, because none of these terrestrial species spread over the ocean on their own (132–135). The phylogenetics of the lizard even show the initial human colonization of the western Pacific, the long pause there, and then, the rapid expansion across the central and eastern Pacific (135). Remains of the Pacific rat, both its bones and the seeds that it gnawed, show human arrival in New Zealand in 1280 CE (136). Additionally, as a final example for the Pacific, sweet potato genetics reveal human travel from South America to Polynesia (137), probably by returning Polynesians.

Animal phylogeographic genetics indicate human movement to and through Europe as well. Land snails moved from Iberia to Ireland (138), mice moved from Norway into Britain (139), and pigs moved into Europe from Turkey by both inland and coastal routes (56).

Cultural Diversity and the Environment

The aspect of phylogeography that I have addressed so far is the spread of a species from its region of origin. As other species spread and subsequently, geographically differentiate, so do humans. Some of the differentiation is, in effect, random genetic drift unrelated to the nature of the environment. In modern terms, "genetic drift", is how Darwin explained regional differences in the human form, because he saw no correlation between environment and anatomy (ref. 140, chap. 11). Of course, we now know that the environment, in fact, strongly influences our anatomy and physiology as many anthropological text books describe.

Far less well known is another aspect of human phylogeography, namely the relation between the nature of the environment and the geographic distribution of cultures (ref. 20, chaps. 5 and 6). The phylogeographic pattern of diasporas from several single origins—northeast Africa to Eurasia, southeast Eurasia to Australia, and northeast Siberia to Americas—allows the equivalent of a repeat experiment on the relation between geography and phylogenetic and cultural diversity. In this section, I review evidence for an influence of the environment on cultural diversity, indeed evidence that the environment influences cultural diversity in the same way as it influences biological diversity or taxonomic diversity.

Tropical Diversity. Humans originated in Africa and eventually spread across much of the world. We did not spread evenly. Throughout the world, in Africa, Eurasia, and the Americas, tropical latitudes are more culturally diverse than nontropical ones, regardless of whether the data are number of hunter–gatherer cultures or number of languages (ref. 20, chap. 5). Most plants and nonhuman animal taxa also show this latitudinal pattern of greater tropical diversity (141). Over 30 biogeographic hypotheses exist for the relation, almost none of which originated with analysis of human cultures (ref. 142, chap. 15). Nevertheless, a long-argued environmentally based hypothesis seems to explain the latitudinal distribution of human cultures, at least in part.

The main facts behind the hypothesis include the well-known year-round high productivity of the tropics where water is sufficient along with the less well-known fact of smaller geographic ranges of tropical cultures, hunter–gatherer cultures, and languages (ref. 20, chaps. 5 and 6). The hypothesis then is that the high year-round tropical productivity allows a population of sustainable size to persist in a small area, a consequence of which is dense packing of cultures (refs. 20, chaps. 5 and 6; 94; and 143–146). The packing could come about by overlap of large ranges. However, human cultures are territorial. Ranges do not overlap, except at high latitudes, where the necessarily large ranges are impossible to defend (ref. 20, chap. 6). The gradient of cultural diversity with latitude and the matching gradient of range size with latitude are not unique to a tropical–nontropical comparison. It occurs within North America too (refs. 20, chap. 5 and 147).

Another hypothesis for regional contrasts in density of cultures is contrast in diversity of habitat (147, 148), which is the case for diversity of species (ref. 142, chap. 15). It is certainly easy to imagine cultures specializing in exploitation of particular habitats and therefore, not extending outside those habitats (149). Indeed, cultures may deliberately separate themselves by exploiting different habitats or exploiting them differentially (150).

This hypothesis and the other hypotheses to explain gradients in diversity are largely correlational. However, humans have themselves in effect performed a phylogeographic experiment to test the productivity hypothesis. They have intensified productivity in cities—in the form of jobs and hence, salaries—that allows purchase of food in a concentrated area instead of its production over an extended area. If level of productivity determines phylogenetic diversity and if phylogeographic concentrations are determined by concentrations of high productivity, rich cities should by one measure of phylogeographic diversity (cultural diversity) be some of the most phylogeographically diverse regions (117).

They are, at least in the United States. Thus, change over time in wages and jobs significantly matched change in diversity of languages in 160 metropolitan areas in the United States over the analyzed 20 y from 1970 controlling for a variety of factors, such as size of the city, sex ratio of workers, and level of schooling (117). As a specific example of the effect, over 300 languages might be spoken in one of the world's largest cities: London (94).

Conclusion. If productivity affects human cultural diversity, it is far from the only influence (143–146, 151). Many other factors can affect diversity, including history. Tropical South America, for example, has an unusually low density of cultures by comparison with tropical Asia and Africa. One reason might be the relatively short period that humans have been in the American tropics. However, another could be the devastating effect of the Old World diseases (smallpox, for example) brought to the New World by invading Europeans from the 15th century on (152, 153). The consequent mass mortality of Native Americans and Amerindians provides a foretaste, perhaps, of both the current global phylogeographic interaction of disease organisms and their human carriers and recipients and also, the disappearance of indigenous languages as majority cultures expand (refs. 20, chap. 8; 154; 155, chap. 12; 156; and 157).

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