ORIGINAL SCIENTIFIC ARTICLE

Studying Cultural Evolution at the Tips: Human Cross-cultural Ecology

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Abstract While human genetic variation is limited due to a bottleneck on the origin of the species ~200 kya, cultural traits can change more rapidly, and may do so in response to the variation in human habitats. Does cultural diversification simulate a natural experiment in evolution much like biodiversity so that cultural divergences and convergences can be interpreted in terms of the differences and similarities of local environments? Or is cultural diversity simply the result of human behavioral flexibility? Although the majority of cultural data comes from the tips of the hominin phylogeny, anthropologists can follow the example of evolutionary ecologists, who often compare the endpoints of phylogenies when that is all that is available. This article compares 97 contemporary indigenous language communities from around the world, and 24 of their cultural traditions, to help determine whether human cultures and their cultural traits are proportionately dispersed, as predicted by the neutral theory of biodiversity, or whether they show non-proportionalities that could be explained with evolutionary reasoning.

Keywords Cultural evolution · Cultural group selection · Human evolution · Cross-Cultural · Behavioral ecology · Evolutionary ecology · Equilibrial ecology

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Introduction

Can natural selection act on cultural variation? Cultural variation is the variation among social groups found in many social animals, from the leaf-tools of the New Caledonian crows and the sponge-tools of the Bottlenose dolphins, to termite-fishing in chimpanzees and the multitude of archeological tools and ornaments, dwellings and institutions of hominid societies (Laland and Janik 2006). The particular variants in these social traditions may not be caused by genetic variation, but they do have histories and can have consequences for an individual's lifetime reproductive output. But how could evolutionary theory work above the levels of genes and individuals, at the level of whole communities? The American evolutionary biologist G.C. Williams (1966) famously promoted the view that evolution happens predominantly through the survival and reproduction of individuals and cautioned biologists to distinguish the evolved features of a group (a fleet herd of deer) from those of individuals (a herd of fleet deer). However, selection among groups has come to be considered an important force in evolutionary biology (Wade 1985; Szathmáry and Demeter 1987; Keller 1999; Okasha 2006; Traulsen and Nowak 2006). Group (e.g. kin) selection helps to explain the variation at all the levels of biological organization created by major evolutionary transitions (Maynard-Smith and Szathmary 1995), from the grouping of genes into chromosomes, and cells into multicellular organisms, to the grouping of multicellular organisms into social groups and colonies. Hypotheses that human behavior also may have evolved adaptations at the group level have been proposed to explain the adaptiveness

of many human cultural traditions (Boyd and Richerson 1985; Sober and Wilson 1998; Wilson 2002).

This paper sets up a background for the evolutionary analysis of cultures by testing the null hypothesis of no evolution. I will first review the neutral theory of biodiversity, which was advanced as a null model in macroecology for predicting patterns of species diversity in the absence of natural selection (Macarthur and Wilson 1963; 1967; Hubbell 2001). I will show how neutral biogeographic patterns apply to humans at the level of whole cultures, and then I will test the geographic distribution of specific cultural traits. The null hypothesis of no evolution at the level of cultural groups is not the nonsense claim that null hypotheses often are. There is a good reason why the endpoints of the human cultural phylogeny may not reflect the action of natural selection, even though in principle cultural group selection could be a powerful force behind human cultural diversity. Human cultural diversity may simply reflect the behavioral flexibility afforded by endothermy, encephalization, and other physiological adaptations that evolved precisely because of the benefits of behavioral flexibility or adaptability in our mammalian ancestors.

Ideally, inferences about evolutionary processes should be made exclusively where the history is completely known from ancestor to descendent. Scientists seeking local patterns in cultural diversity have benefited from the abundant knowledge that exists about local population histories (Borgerhoff Mulder 2001; Borgerhoff Mulder et al. 2001). Yet, for scientists seeking global patterns in cultural diversity, there are unfortunately no clear ancestor–descendent relationships among the world's ~300 language families, despite the fact that all humans belong to a single species of relatively small genetic diversity. The reason is that human diversification in the Pleistocene happened considerably sooner than the 8,000±2,000-year limit on language's historical signal (Nichols 1992) and most likely involved multiple dispersals out of Africa from an already structured set of populations (Lahr and Foley 1994). Although methods have been introduced to extend the time-depth of language history reconstruction (Dunn et al. 2005), the unknown relationships among existing language families is an insurmountable problem for creating a global phylogenetic tree for cultural evolution based on language. Fortunately, the comparative method can still be applied even when the only data available are from extant groups at the tips of a phylogeny. The design of comparative research is simple. Examples of a phenomenon (e.g. culture, language, population, species) are cases that are similar in some respects and are different in other respects. The goal is to find out why the cases are different, to reveal the general underlying causes that generate variation. Anthropologists can follow the example of evolutionary ecolo-

gists, who often compare the endpoints of phylogenies when that is all that is available. This paper compares 97 contemporary indigenous language communities from around the world and 24 of their cultural traits to determine whether they are neutrally dispersed (randomly dispersed with the exception of spatial constraints and latitudinal gradients) as predicted by the neutral theory of biodiversity, or whether they do in fact show any deviations from neutral expectations that can be explained with evolutionary reasoning.

The Null Hypothesis: Human Culture in Equilibrium

The neutral theory of biodiversity (Macarthur and Wilson 1963; 1967; Hubbell 2001) is a theory about the "ecological drift" of biodiversity, both in terms of an area or community's number of species (the species richness), and in terms of its makeup (the relative species abundance). Using the assumption that all individuals of every species are ecologically equivalent within the trophic level of their food web, the neutral theory can predict these biodiversity patterns on the basis of demographic stochasticity alone (random speciation and extinction, random migration), independent of species interactions and niche adaptation. Central to the neutral theory's predictions about biodiversity is that an equilibrium state is established by the fact that "Earth and its limiting resources are permanently and completely saturated with organisms" (Hubbell 2001, p.152), because the proposed equilibrium between immigration and emigration, speciation and extinction is inspired by the constant scaling of species richness with geographical area at similar latitudes. How could the dynamic equilibrium of species richness and geographic area apply to human cultures and their cultural traits?

Given the relative proportionality of latitudinal distribution among the continents, the ecological theory of equilibrium leads us to expect that human cultural groups like language communities, by analogy, with the populations or species of non-human taxa, should be proportional with the total human geographical range, namely, all continents but Antarctica. In other words, the neutral theory leads us to expect that the human geographic range is saturated by a maximum density of human cultures. It is necessary to take latitude into account because the expectation of equilibrium is at a smaller-than-global scale. At the global scale, the strongest predictor of biodiversity is latitudinal gradients, which relate to primary productivity, environmental variability, and, potentially, the species-area correlation as well (Willig et al. 2003; Hillebrand 2004). In high latitudes, speciation rates appear to be low relative to extinction rates, whereas at the equator, speciation rates appear to be high relative to extinction rates, and so, species

accumulate near the equator. Several authors have also noted a latitudinal gradient in the worldwide density of human languages, with higher numbers towards the equator than towards the poles (Nettle 1998; Collard and Foley 2002; Mace and Pagel 1995), paralleling the gradient seen in biological species richness. Humans, like other species, appear to be especially abundant nearer the equator, although this is not surprising given that most hominid species are thought to have arisen in subtropical regions in and around Africa. Figure 1 shows percentages of total living languages per continental region cited by the *Ethnologue* language database (Gordon 2005; see http://www.ethnologue.com/ethno_docs/distribution.asp?by=area) plotted against the percentage of total terrestrial area, excepting Antarctica (from Grosvenor 1966), and fit with an arbitrary regression-type line. The major continental regions plotted hold roughly similar latitudinal distributions from low to high latitudes.

Although a proportional distribution is expected between the geographic areas of the continents and the number of language groups they maintain, two regions, Oceania and Africa, maintain more groups per area, while one region, the Americas, although it is the largest of the regions compared, maintains fewer language groups. The prehistory of human dispersal and migration across the continents can help describe the reasons for departure between language group abundance and geographical area in three out of five data points. In areas like the Americas that were initially reached at later dates, less time to diversify could have led to unequal proportions of cultures to area. Alternatively, the recent Holocene history of expanding agricultural groups could have disrupted the ecological equilibrium around centers of agricultural innovation. These explanations should not be dismissed as reflecting historical circumstances alone. The differential expansion and marginalization of cultural groups is an evolutionary signal. Although the expansion
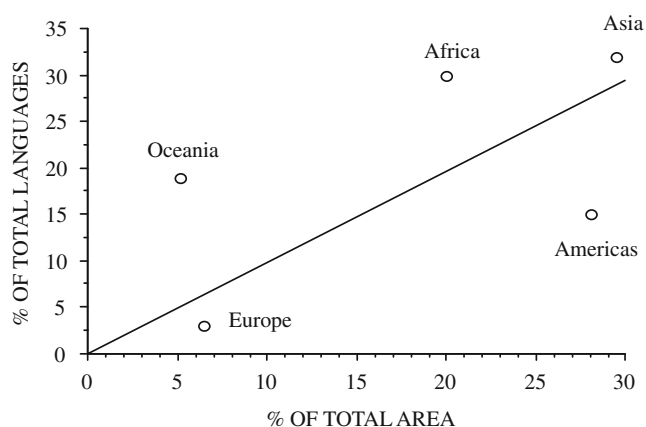
and retraction of group size cannot produce group-level adaptations without the colonization of *new* groups, it nonetheless has been considered sufficient basis for the action one of the two forms of multi-level selection ("Multi-Level Selection type 1" (MLS1) Damuth and Heisler 1988; Okasha 2006, elsewhere called "trait-group selection" Wilson 1975; 1980, "patch selection" Van Valen 1980, and "false or soft group selection" Mayr 1997). Individual-level adaptations can occur during this weak form of group selection, however, by virtue of group membership, as in the evolution of lactase evolution under the expansion of dairy farming (Durham 1991).

A Global Comparison of Cultural Trait Distributions

Whereas using the neutral theory of biodiversity at the level of cultural diversity establishes the expectation for a global relationship among human cultures as a function of geographic area and latitude, the geographic dynamics of specific cultural traits is also of interest. Claims that particular cultural traits like religious doctrines (Wilson 2002) may have evolved as human group-level adaptations can be ruled out if they obey the expectation of neutral distribution around the globe. Statistical analysis was carried out to examine the distribution of specific cultural traits across continental regions. The goal was to assess whether the variation within cultural traits is statistically equivalent across regions (and if so, to what extent) or if regions show heterogeneous distributions of cultural traits.

A total of 97 well-circumscribed linguistic groups of varying size, geographical scope, and linguistic/genealogical origin (see Fig. 2) held enough ethnographic description of cultural traits to be considered sufficiently informative for analysis. See Appendix A for a complete list of the language groups that were compared, classed into language families and showing a measure of their representativeness. Cultural data were recorded directly from ethnographic compendia and databases, or else deduced or inferred from descriptions in the literature and given original codifications (see Appendix A). A primary source for these is the Human Relations Area Files (HRAF) ethnographic search engine. Socio-economic data were then added from the *Ethnographic Atlas*, a database of 1,167 language groups first compiled by Murdock (1962–1980) in 29 successive installments of the journal *Ethnology*. A running update of the database is edited as a supplement to the journal *World Cultures*. Data were assigned to four continental regions to reflect natural barriers to migration and dispersal: (1) Africa (south of the Saharan desert), (2) Europe (and Asia west of the Himalaya Mountains), (3) the Americas, and (4) Asia east of the Himalayan Mountains, including the Pacific islands.

Fig. 1 Languages per geographic area in five continental regions. The central line is for general reference only

Fig. 2 Language groups under analysis. The 97 language groups under analysis shown on a world map

Scale: 1:241597371 at Latitude 0°
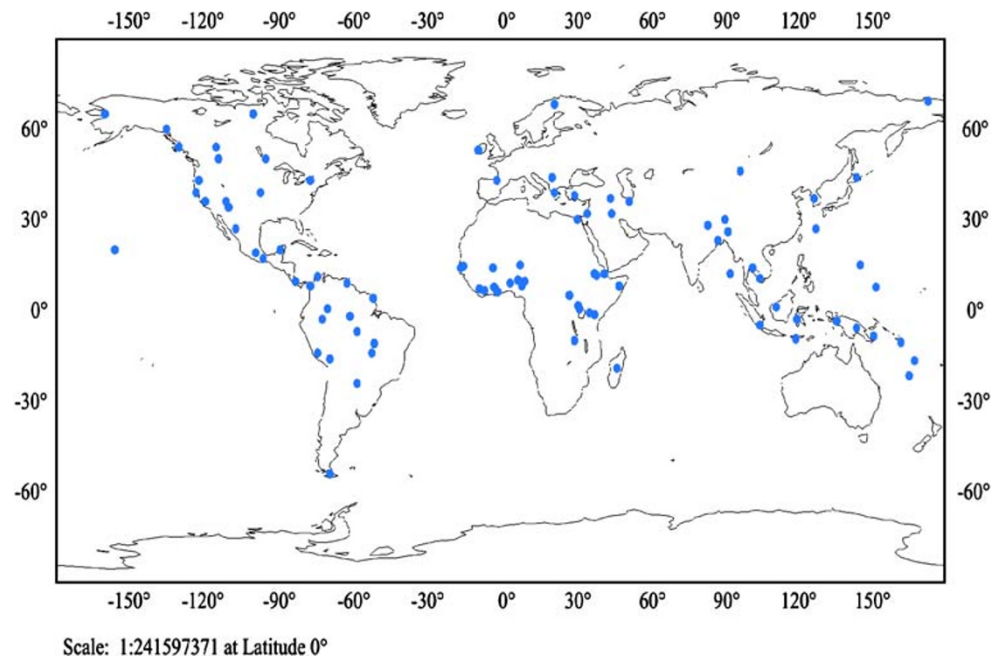
The null hypothesis that there is independence among regions with respect to cultural trait distributions was tested using the chi-square test. The chi-square (χ^2) test is a test of independence, also known as a test of association, used in this case non-parametrically, though suitable for parametric or non-parametric distributions. It tests whether each possible outcome on a contingency table is equally likely, e.g., that a culture's lucky number is equally likely to be 3 or 4 or 7 whether the culture is situated in the Americas, in Eurasia, in Subsaharan Africa, or in East Asia/Oceania. To further address the strength of association or non-independence, if any, Cramer's V was used, which has a range of 0 (*NS*) to 1 (association). This measure is a modification of the Phi Coefficient (a standard measure of association for 2×2 contingency tables), allowing it to be used in the comparison of variables of different numbers of categories (although it should only be done in relative, not absolute terms), and in the analysis of contingency tables larger than 2×2 (Siegel and Castellan 1988).

Results

The chi-square analyses revealed that the distributions of many of the variables under analysis are not fully independent from geographical region, at the scale of the four continental regions compared. The results of analyses for each cultural trait can be seen in Appendix B. Out of the 24 cultural variables tested, only eight varied without significant association with geographic region (at the level of $p < 0.05$). But instead of referring exclusively to the chi-

square level of significance, Cramer's V provided a measure of how closely associated (on a range from 0 to 1) the traits are with respect to geographic region. Their level of association is low on average, reflected in an average Cramer's V of 0.353.

Discussion

Eight cultural variables violated the null hypothesis by being strongly associated with geographical region ($p < 0.001$). Two particularly geographically sensitive traits under analysis regard language. *Language Family*, though more of a phylogenetic marker than a cultural trait because of the extremely conservative inheritance of language, is expected to reflect the constraints on cultural traits that are inherited vertically, from parents to offspring, rather than horizontally, within a generation. Language is, therefore, a trait that varies spatially due to migration and dispersal rather than diffusion between cultures. Since populations tend to migrate and disperse within circumscribed areas of the earth, language families tend to be localized to single continental regions.

The *Number of Languages In Language Families* was also found to be geographically uneven. This variable corresponds to the range between language isolates, the last extant members of a language family like Ainu or Basque, to particularly populous language families, like Niger-Kongo or Malayo-Polynesian (see Appendix A). The concentration of large and small language families in particular regions reveals a clear disruption in the equilibrium of cultures

worldwide. The explanation for this is marginalization, as seen in the pattern of innovation and subsequent colonization, following particularly productive inventions such as agriculture, that lead to differential expansion. Cultural group expansion also explains the remaining six highly geographically sensitive traits under analysis: *Mode of Subsistence, Monotheism, Borrowed vs. Invented Writing System, Subsistence Economy, Agricultural Intensity,* and *Religious Influence*. For instance, historically, monotheism expanded from its point of origin in the Middle East, explaining the trait's lack of proportionality between the Middle East and other regions around the globe. This deviation from the neutral theory's expectation of equilibrium lends support to the hypothesis of Wilson (2002) that religious doctrine is subject to an evolutionary process.

On the other hand, the six variables that because of their low Cramer's *V*, most clearly upheld the null hypothesis of equilibrium among states of globally distributed cultural traits, for instance the *Gender of Mythical/Legendary Entities* and *Number System Base*, confirm the prediction of equilibrium among cultural trait state distributions around the globe. These traits exemplify the independence of cultural traits from geographic differences and fall into either of two ironically quite opposite, classes: (1) cultural traits may express variability that is universal to all humans independent of the local environment. Alternatively, (2) cultural traits may be so plastic as to have much of their total variability explored either by chance or in response to local environments. These traits conform to the conventional definition of culture as a highly variable, often arbitrary phenomenon that is the result of human behavioral flexibility.

Are Cultures Too Unique for Comparison?

Potential pitfalls of these analyses include problems with comparing cultures in general. The particular variables and codes used in analysis here, as well as the categorization of cultural traits in principle, are vulnerable to inaccuracy on two counts: miscategorizing out of anachronism, bias, or imprecision, and miscategorizing because of an essential incomparability of cultures or cultural traits. Avoiding anachronism, bias, and imprecision, including categorization itself where there exists a continuum, is an ongoing scholarly task requiring sensitivity and vigilance. Whereas avoiding inaccuracies is simply constitutive of scholarship, the second potential problem of incomparability among cultures would pose a fundamental barrier to any methodological strategy, and so addressing this is of fundamental importance to cross-cultural analysis.

The larger challenge as it is usually posed, of a fundamental incomparability among cultures, questions whether cultures or traditions may be intrinsically incom-

parable because of different underlying histories or different overlying functions. The steps taken towards organizing society around key traditions, for example agriculture, are not universal, nor possibly are the precise functional reasons for them to persist. However, the research problem can be restated in statistical terms, to ask whether the steps taken around such major organizational features of a society are often correlated with certain other features. A more concrete challenge, however, is that the groups being compared are not always unitary along the variables of interest. Groups vary within themselves according to social contexts related to age, status, and gender, and according to functional contexts such as building, food procurement and preparation, worship, mourning, and wedding ceremonies. Given that many variants of cultural traits can be seen to depend on contexts that vary in time and space within cultures, the choice of single variants of cultural traits to represent their culture is made especially difficult. Whether by chance or by design, different variants are often clearly employed for different activities. For example, the Duke of York Islanders "usually count in tens but count coconuts, taro, and yams by fours, and have a special set of terms for counting *diwara* ("shell money") in quantities of sixty" (Bowers 1977). Until such fine-grained variation within cultures can be rightfully compared, cross-cultural researchers must rely on the precedents of using individual reports to represent group-level traits in psychology and cross-cultural anthropology (Triandis 1996), and although the costs of doing so are noisy data and a lower rate of significance in statistical tests, this is often a smaller price to pay than the assumption that large-scale, quantitative research cannot be done.

Part of the resistance in anthropology to scientific generalizations is that they can, and have been, misused. The assumption that history equals progress dominated early anthropological study as pervasively as did the sun's apparent rise and fall in pre-Copernican astronomy. However, indigenous human cultures of the past and present are longer seen as steps on a single ladder of global social progress reminiscent of Aristotle's *Scala Naturae*. Evolutionary theory has offered anthropologists a new appreciation of global diversity through local adaptation. But evolutionary claims are not the only avenue for explaining cultural diversity, and should not be, given humanity's recent origin, small genetic diversity, evolved behavioral flexibility, and tools for adapting within generations without the need for true multigenerational evolution by natural selection.

Appendix A: Cultural Trait Values

Quantitative Variables

Highest recorded base of the culture's numeric system (≤5) e.g. base 5, decimal, *duodecimal, vigesimal*

Highest number to which people count (up to 10,000) or number meaning "many."

Dominant recorded ritual or lucky number.

Qualitative variables

N	Total	Language family	Language group
24	NA	Language isolates; No known relatedness	Ainu, Andamanese, Palikur, Basque, Pawnee, Atroari, Ona, Chukci, Pomo, Iroquois, Japanese, Korean, Tzeltal, Masaai, Zapotec, Yagua, Inca, Stoney, Thai, Tukano, Saami, Warao
18	1489	Niger–Congo	Akamba, Ashanti, Azande, Banyoro, Bemba, Berom, Bete, Dan, Dogon, Fanti, Fulah, Ganda, Koro, Kulango, Luba, Serer, Tiv, Wolof, Yasgua, Yoruba
2	47	Na-Dene	Tlingit, W. Apache
3	62	Uto-Aztecan	Aztec, Hopi, Tarahumara
2	38	Algonquian	Blackfoot, E. Ojibwa, Ojibwa
3	22	Chibchan	Cuna, Kogi, Talamanca
8	372	Afro-Asiatic	Amhara, Babylonian, Egyptian, Hausa, Hebrew, Somali
12	1239	Malayo-Polynesian	Api, Caroline Islanders, Chuuk, E. Toradja, Hawaiian, Houailou, Iban, Kodi, Malagasy, Malekula, Tikopia, S. Toradja, Trobriand Islanders
2	32	Macro-Ge	Karaja, Xavante
2	372	Austro-Asiatic	Khasi, Khmer, Santal
3	33	Penutian	Klamath, Lake Yokuts, Tsimshsian, Yokuts
7	443	Indo-European	Bengali, Croat, Greek, Kurdish, Maldivian, Roman, Serb
2	70	Tupi	Guarani, Munduruku
2	11	Eskimo-Aleut	Copper Inuit, Inupiaq
3	365	Sino-Tibetan	Chepang, Chinese, Tibetan
2	552	Trans-New Guinea	Kapauku, Kewa
2	65	Altaic	Turkish, Mongolian

N	Language family size
30	Thousands of members
11	Five or less members (language isolate)
32	Between five and a hundred members
24	Hundreds of members
0	Missing data

N	Religious influence
24	None
55	Babylonian Zoroastrian, Judeo-Christian or Muslim
11	Buddhist or Hindu
7	Missing data

N	Method of counting or tallying
5	Total tool using, including words and stylized inscriptions
31	Some non-tool object use—body parts, pebbles, sticks
61	Missing Data

N	Recorded preference, ritual or otherwise, for even or odd numbers
32	Even
29	Odd
36	Missing data

N	Degree of Monotheism (adapted from "high gods" Gray 1999)
30	Absent or not reported
16	Not active in human affairs
7	Active in human affairs but not supportive of human morality
20	Supportive of human morality
24	Missing data

N	Grammatical system
22	OV
30	VO
45	Missing data

N	Gender of dominant deities or mythical heroes
27	Absence of female deity/hero
29	Presence of female deity/hero
41	Missing data

N	Predominant calendar type
64	Strictly astronomical or otherwise empirical (e.g. lunar)
8	Arithmetic (e.g. intercalated, solar)
25	Missing data

N	Primary indigenous writing system
56	Alphabet (symbols—letters—depict sounds)
21	Syllabary or syllabic alphabet (symbols depict syllables)
6	Systematic logograms/ideograms (symbols depict words)
14	Missing data

N	Written system of communication
53	No use of indigenous alphabet or syllabary—borrowed
44	Invented an alphabet or syllabary (independently or through stimulus diffusion)
0	Missing data

N	Dominant mode of subsistence
26	Hunting/gathering
7	Pastoralism
61	Agriculture
3	Missing data

N	"Intensity of Agriculture" (from Gray 1999)
14	No agriculture
2	Casual agriculture, incidental to other subsistence modes
32	Extensive or shifting agriculture, long fallow, and new fields cleared annually
5	Horticulture, vegetal gardens or groves of fruit trees
17	Intensive agriculture, using fertilization, crop rotation, or other techniques to shorten or eliminate fallow period
16	Intensive irrigated agriculture
11	Missing data

N	Dominant pattern of descent
33	Patrilineal
14	Matrilineal
43	Ambi/duo/bilateral or mixed
7	Missing data

N	"Transfer of Residence at Marriage: After First Years" (from Gray 1999)
58	Wife to husband's group
12	Couple to either group or neolocal
20	Husband to wife's group
7	Missing data

N	"Domestic Organization" (from Gray 1999)
11	Independent nuclear family, monogamous
13	Independent nuclear family, occasional polygyny
2	Independent polyandrous families
2	Polygynous: unusual co-wives pattern
8	Polygynous: usual co-wives pattern
8	Minimal (stem) extended families
45	Small or large extended families
0	Missing data

N	"Largest Cognatic Kin Group" (from Gray 1999)
23	Bilateral descent
15	Kindreds: ego-oriented bilateral kin groups
1	Ambilineal descent: lacking true ramages
3	Ramages: ancestor oriented ambilineal groups
49	Unilineal descent groups
6	Missing data

N	"Kin Terms for Cousins" (from Gray 1999)
26	Hawaiian-type
14	Iroquois-type
17	Eskimo-type
5	Omaha-type
8	Descriptive-type
7	Crow-type
3	Mixed
17	Missing data

N	"Community Marriage Organization" (from Gray 1999)
14	Demes, not segregated into clan barrios
13	Segmented communities without local exogamy
36	Agamous communities
8	Exogamous communities, not clans
2	Segmented communities, localized clans, local exogamy
11	Clan communities, or clan barrios
13	Missing data

Appendix B: Cultural Trait Association with Regions

The results of chi-square (χ^2) analyses.

The level of association between cultural traits and geographic regions is low on average, with an average Cramer's V of 0.353, which has a range from 0 to 1

Cultural variability across geographic regions	P value (χ^2)	Cramer's V
Gender of legendary entities	<0.921	0.094
Number system base	<0.627	0.138
Highest recorded indigenous count	<0.392	0.244
Descent pattern	<0.094	0.245
Community marriage organization	<0.364	0.254
Largest cognatic kin group	<0.078	0.267
Marriage residence pattern	<0.040	0.271
Descent, major type	<0.035	0.312
Mode of subsistence	<0.001	0.326
Writing system type	<0.006	0.333
Kin terms for cousins	<0.049	0.347
Domestic organization	<0.003	0.365
Calendar type	<0.014	0.384
Grammatical system	<0.050	0.388
Dominant lucky or ritual number	<0.603	0.393
Method of counting/tallying	<0.117	0.405
Monotheism	<0.001	0.437
Borrowed or invented writing system	<0.001	0.450
Preference for even or odd numbers	<0.005	0.465
Subsistence economy	<0.001	0.475
Intensity of agriculture	<0.001	0.481
Religious influence	<0.001	0.532
Number of languages in language families	<0.001	0.602
Language family	<0.001	0.853

References

Borgerhoff Mulder M. Using phylogenetically based comparative methods in anthropology: more questions than answers. Evol Anth. 2001;10:99–111.

Borgerhoff Mulder M, George-Cramer M, Eshelman J, Ortolani A. A study of East African kinship and marriage using a phylogenetically-based comparative method. Amer Anth 2001;103(4):1059–82.

Bowers N. Kapauku numeration: reckoning, racism, scholarship, and Melanesian counting systems. The Journal of the Polynesian Society 1977;86:105–16.

Boyd R, Richerson P. Culture and the evolutionary process. Chicago, IL: University of Chicago Press; 1985.

Collard I, Foley R. Latitudinal patterns and environmental determinants of recent human cultural diversity: do humans follow biogeographical rules? Evolutionary Ecology Research 2002; 4:371–83.

Damuth J, Heisler IL. Alternative formulations of multilevel selection. Biology & Philosophy 1988;3:407–30.

Dunn M, Terrill A, Reesink G, Foley R, Levinson S. Structural phylogenetics and the reconstruction of ancient language history. Science 2005;309:2072.

Durham W. Coevolution: genes culture and human diversity. Stanford, CA: Stanford University Press; 1991.

Gordon RG Jr. (ed.) Ethnologue: languages of the world. 15th ed. Dallas, Tex: SIL International. Online version: http://www.ethnologue.com/; 2005.

Gray P. (ed) A corrected ethnographic atlas. World Cultures 1999;10:94–144.

Grosvenor G. National Geographic Atlas. Washington, D.C.: The National Geographic Society; 1966.

Hillebrand H. On the generality of the latitudinal diversity gradient. Am Nat 2004;163:192–211.

Hubbell SP. The unified neutral theory of biodiversity and biogeography. Princeton, NJ: Princeton University Press; 2001.

Keller L. (ed) Levels of selection in evolution. Princeton: Princeton University Press; 1999.

Lahr M, Foley R. Multiple dispersals and modern human origins. Evol Anth 1994;3:48–60.

Laland K, Janik VM. The animal cultures debate. TREE 2006; 21:542–7.

Macarthur R, Wilson E. An equilibrium theory of insular zoogeography. Evolution 1963;17:373–87.

Macarthur R, Wilson E. The theory of island biogeography. Princeton, NJ: Princeton University Press; 1967.

Mace R, Pagel M. A latitudinal gradient in the density of human languages in North America. Proc Roy Soc B 1995;261:117–21.

Maynard Smith J, Szathmary E. The major transitions in evolution: from prebiotic chemistry to the origins of society. Oxford: Oxford University Press; 1995.

Mayr E. The Objects of selection. PNAS 1997;94:2091–2094.

Murdock G. The ethnographic atlas. Ethnology 1962–1980;1–19.

Nettle D. Explaining global patterns of language diversity. Journal of Anthropological Archaeology 1998;17:354–74.

Nichols J. Linguistic diversity in space and time. Chicago, IL: University of Chicago Press; 1992.

Okasha S. Evolution and the levels of selection. New York: Oxford University Press; 2006.

Siegel S, Castelan NJ Jr. Nonparametric statistics for the behavioral sciences. 2nd ed. New York: McGraw Hill; 1988.

Szathmáry E, Demeter L. Group selection of early replicators and the origin of life. J Theor Biol. 1987;128:463–86.

Sober E, Wilson DS. Unto others: the evolution and psychology of unselfish behavior. Cambridge, MA: Harvard University Press; 1998.

Traulsen A, Nowak MA. Evolution of cooperation by multi-level selection. Proc. Natl. Acad. Sci. USA 2006;103:10952.

Triandis H. The psychological measurement of cultural syndromes. American Psychologist 1996;51:407–15.

Van Valen L. Review of the natural selection of populations and communities by David Sloan Wilson. Evolutionary Theory 1980;4:231.

Wade MJ. Soft selection, hard selection, kin selection, and group selection. Am Nat 1985;125:61–73.

Williams GC. Adaptation and natural selection. Princeton, NJ: Princeton University Press; 1966.

Willig M, Kaufman D, Stevens R. Latitudinal gradients of biodiversity. Ann Rev 2003;34:273–309.

Wilson DS. A general theory of group selection. Proceedings of the National Academy of Sciences 1975;72:143–46.

Wilson DS. The natural selection of populations and communities. Menlo Park, CA: Cummings; 1980.

Wilson DS. Darwin's cathedral: evolution, religion and the nature of society. Chicago, IL: University of Chicago Press; 2002.