

Natural selection and cultural rates of change

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It has been claimed that a meaningful theory of cultural evolution is not possible because human beliefs and behaviors do not follow predictable patterns. However, theoretical models of cultural transmission and observations of the development of societies suggest that patterns in cultural evolution do occur. Here, we analyze whether two sets of related cultural traits, one tested against the environment and the other not, evolve at different rates in the same populations. Using functional and symbolic design features for Polynesian canoes, we show that natural selection apparently slows the evolution of functional structures, whereas symbolic designs differentiate more rapidly. This finding indicates that cultural change, like genetic evolution, can follow theoretically derived patterns.

canoe design | cultural evolution | Polynesia | signatures of selection

It has been claimed that a scientific theory of cultural evolution is not possible because human beliefs and behaviors do not follow predictable patterns (1). Critiques of cultural evolution from within science object that analogies with genetic evolution do not hold (2), and culture is altered instead by a series of contingent historical events (3, 4). Biologists have developed theoretical models to understand patterns in genetic evolution, revealing evolutionary relationships, population bottlenecks, genes under selection, and even past human migrations (5–7). Similar theoretical models for human cultural evolution have been developed, beginning with work by Cavalli-Sforza and Feldman in the 1970s (8) and data gathered to test their utility (9). Cultural evolution here refers to changes over time in the nongenetic information possessed by human societies, as affected by processes such as transmission and innovation. But, does cultural change really exhibit patterns that can be understood by using theoretical models?

It has been hypothesized that cultural characteristics that are tested against the environment will evolve at a faster rate than cultural characteristics that are not (10, 11). An important recent report showed that in languages, frequently used words evolve more slowly (12). Biological data indicate that proteins that have a greater bearing on fitness evolve at a slower rate because of the constraining force of negative (purifying) selection (13). Negative selection removes deleterious mutations, reducing variability, rate of change, and divergence between populations (14). On the other hand, genes experiencing positive selection may evolve more rapidly (15). For example, genes coding for sea snail venom appear to have diverged rapidly under positive selection (16). Proposed molecular signatures for positive selection include higher between-population differences, higher frequency of derived alleles, reduction of diversity within a population or species, and longer haplotypes because linked traits are carried along in selective sweeps (15, 17, 18). In the absence of selection, genetic evolution takes place via mutation and drift, producing random changes in trait frequency (19).

How might this apply to cultural evolution? Archaeologists have suggested that functional elements of cultural artifacts may be subject to natural selection and convergence, whereas stylistic elements may be selectively neutral and thus more useful for detecting cultural affinities and chronological change (20–22). Human cultural groups, like genetic demes, live in different environments and have a high rate of within-group exchange of

traits but also have the potential for some exchange with other groups through migration or cultural borrowing. Cultural adaptations central to a society tend to be passed along vertically (within families and groups) (11, 23–25).

Cultural traits that are selectively neutral should change at a rate determined by the cultural equivalents of mutation (innovation) and drift. If a cultural trait affects the survival and reproduction of its bearers, natural selection should affect rates and directions of change. (Note that natural selection, in this context, acts on differentials based on the adaptive value of cultural, not genetic, traits.) Negative or purifying selection should result in less within-group diversity, a slower rate of change, and, thus, less divergence between related groups. Positive selection should also result in less within-group diversity but a faster rate of change leading to greater differences between groups. The outcomes under both positive and negative selection could be affected by population expansion, migration, cultural exchange, or cultural selection (which may oppose natural selection; consider, for example, the cultural promotion of smoking).

In this study, we ask whether cultural traits bearing on survival and reproduction show signatures of selection by changing at a different rate from those that do not. If no such differences are apparent, then it is hard to make the case that systematic evolutionary processes are at work. It is possible, of course, that certain beneficial traits were under positive selection whereas others were being selected against during the time frame of our analysis. Without specific information on the history of each canoe design, it is doubtful that these could be distinguished. Molecular biology techniques for identifying traits under positive selection require knowledge of genetic linkage disequilibrium (18); we do not have analogous information for canoe traits. The question we can answer is whether the system as a whole was under a regime of positive selection (in which many new and beneficial traits are increasing in frequency) or of negative selection (in which many of the existing beneficial traits are protected by selection against new, less beneficial variants).

Finding cultural traits with which to test such ideas proved difficult. The traits we settled on were the design elements of canoe building across Polynesian societies. We have since learned that the French philosopher Alain (Émile-Auguste Chartier) in 1908 proposed that boat design would be subject to natural selection (26). “Tout bateau est copié sur un autre bateau. . . Raisonons là-dessus à la manière de Darwin. Il est clair qu’un bateau très mal fait s’en ira par le fond après une ou deux campagnes, et ainsi ne sera jamais copié. . . On peut donc dire, en toute rigueur, que c’est la mer elle-même qui façonne les bateaux, choisit ceux qui conviennent et détruit les autres” (pp

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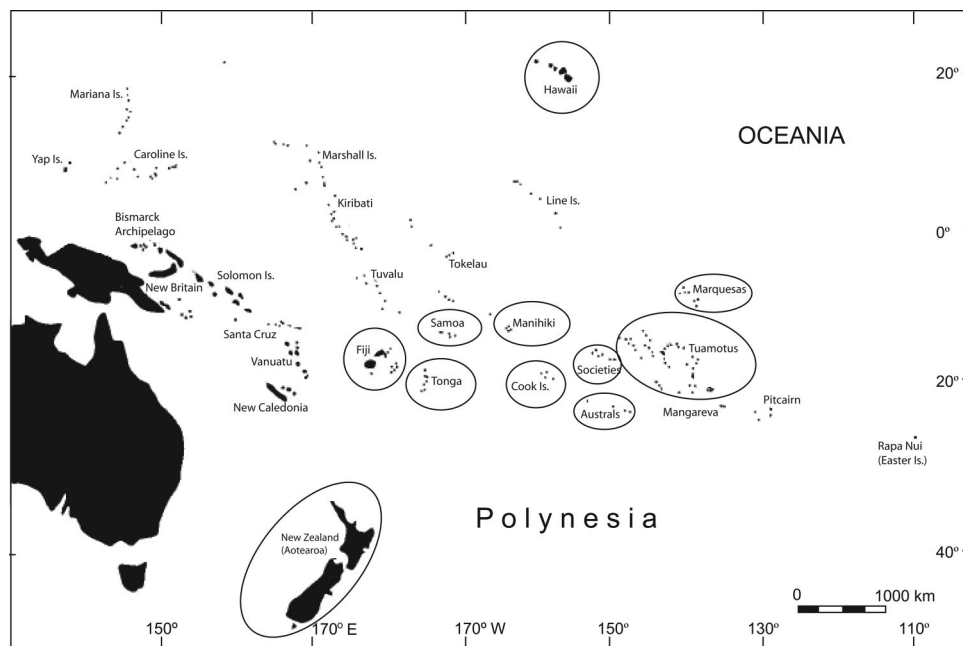


Fig. 1. Ten Polynesian island groups plus Fiji were studied. The Fijian archipelago is thought to have been the jumping-off point for the colonization of Polynesia ($\approx 2,500$ – $3,000$ years ago) with New Zealand (Aotearoa) being the last major island to be settled. See [SI Table 1](#) for a list of the archipelago names and associated major islands and alternate names for each island group.

41–42). [Every boat is copied from another boat. . . Let's reason as follows in the manner of Darwin. It is clear that a very badly made boat will end up at the bottom after one or two voyages, and thus never be copied. . . One could then say, with complete rigor, that it is the sea herself who fashions the boats, choosing those which function and destroying the others. (Translated by D.S.R.)]

Polynesia is a useful model system for looking at cultural development because the region was originally colonized by one cultural group ($\approx 2,500$ – $3,000$ years ago) that then radiated out into a set of related societies in relative isolation (27–29). Descriptions of canoe design had been compiled from original accounts by early explorers and from more recent observations of museum pieces and published by Haddon and Hornell in 1936–1938 (30). Using these descriptions, we identified and coded canoe design traits described for 10 Polynesian island groups plus Fiji (see Fig. 1). These traits were divided into functional design elements (those that may have a bearing on

whether the boat's occupants would survive a trip; see Fig. 2) and symbolic design elements (aesthetic, social, and spiritual decorations that presumably have no differential effect on survival from group to group; see Fig. 3).

Island-by-island cultural distances based on these functional and symbolic canoe traits could then be compared with answer our question: Do functional canoe traits change at a different rate from that of symbolic traits? The null hypothesis would be that they change at a similar rate, and the potential of functional canoe traits to affect outcomes of survival, migration, and reproduction leaves no signal. A significant difference in rate of change between the two types of traits, on the other hand, would indicate that different real-world outcomes associated with functional traits may play a role in cultural change. This difference would support the value of approaching cultural change from an evolutionary perspective.

Our expectation was that the functional traits would change at a significantly different rate from that of symbolic traits. This

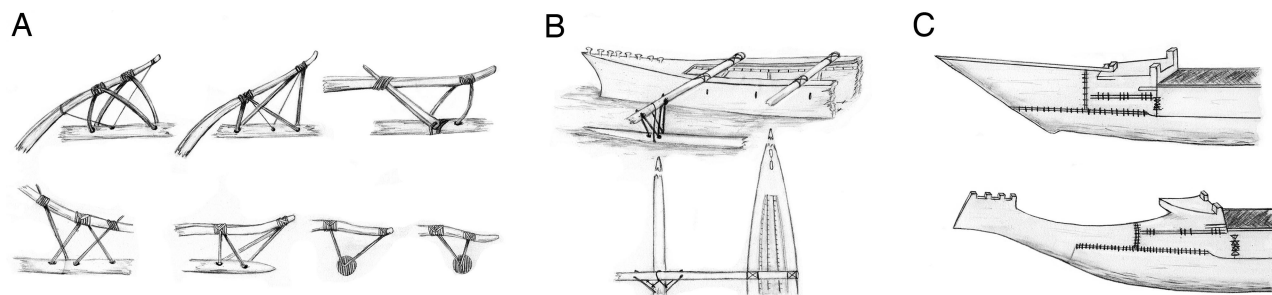


Fig. 2. Functional traits for Polynesian canoes may affect whether a voyage for fishing, warfare, or colonization succeeds. (A) Detail of outrigger attachments on a Tahitian canoe. Shape of the boom and method of lashing varied greatly. They may have had important implications for the types of waves encountered, or may have been constrained by availability of materials, but this knowledge has not been preserved. (B) Samoan canoe "sewn" together with sennit (coconut fiber cord). This particular hull had a narrow keel and strengthening "ribs," presumably to provide speed and stability in rough conditions. (C) Canoe from Manihiki showing pattern of sewn washstrake pieces (necessary when large tree trunks are not available for hull construction). Every island group studied had at least one type of canoe hull made from a single large tree trunk, but most groups also had designs with built-up parts, usually sewn with sennit but some attached with woodworking joining techniques. [Drawings by Darryl Wheye (Science Art). Modified from Haddon and Hornell (30).]

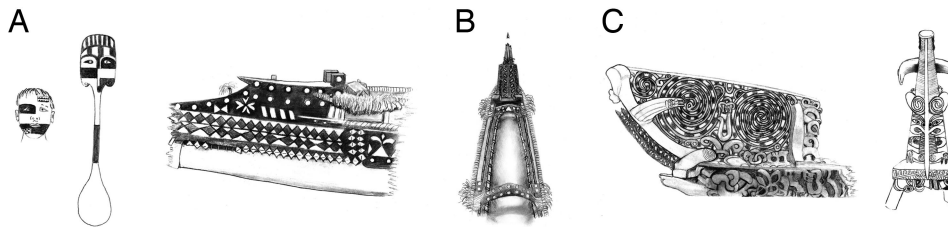


Fig. 3. Symbolic traits for Polynesian canoes presumably have no differential effect on survival from group to group. (A) Painted paddle from Rapanui (Easter Island) alongside face tattoo from the Marquesas. Similar symbolism probably indicates phylogenetic or cultural exchange relationships between the islands. (B) Canoe from Manihiki decorated with inlaid shell. (C) Carved figurehead on Maori war canoe (New Zealand). Marked differences in canoe profiles may have facilitated long-distance identification of parties during warfare. [Drawings by Darryl Wheye (Science Art). Modified from Haddon and Hornell (30).]

rate could be either faster or slower, depending on whether they were generally under positive or negative selection during the time frame under consideration. It is possible that positive selection could drive rapid change through global selection of canoe design traits that confer advantage everywhere, or drive diversification through local selective forces; i.e., different social demands for warfare, long-distance voyaging, or short fishing trips, and different environmental variables such as the hazards of navigating fringing reefs versus deep water, or weather-related currents and wave conditions. Both global and local selection were probably at work; specifying detailed expectations in this area is difficult because both social and climate-related variables would have been changing during the long time frames of interest.

Results and Discussion

A two-way Mantel test on the functional versus symbolic trait Jaccard distance matrices was performed to determine the extent of correlation in patterns of change between the functional and symbolic canoe design traits (see *Methods*). This test, which looks for correlations between matrices, identified no significant correlation between the two sets of Jaccard distance measures across the island pairs ($r = 0.00108$; $P = 0.5029$). This indicates that the functional and symbolic traits did not covary from society to society but instead followed relatively independent trajectories.

To assess whether rates of change were similar or different, we assumed that a faster rate of change would result in greater island-by-island cultural distances as measured by the Jaccard distance. We used the Sign test, a nonparametric test for differences between two groups of paired observations, to compare the functional and symbolic trait distance matrices for this difference. The Sign test seems to indicate a highly significant difference in distances, and thus rates of change, between the functional and symbolic traits ($P = 1.3088 \times 10^{-8}$ for the two-tailed test). However, because internal correlations exist between values within each distance matrix, probabilities derived from this and other standard statistical tests may not be valid.

To check this result against a probability distribution that takes into account these internal correlations, a randomization was performed on the choice of traits assigned as functional or symbolic, and a frequency distribution of Wilcoxon signed-rank test statistics was developed for the recalculated distance matrices [see [supporting information \(SI\) Fig. 4](#)]. A similar or more extreme test statistic value was obtained only 56 times in 10,000; thus, results are still significant, but only at the 0.01 level.

This result indicates that functional traits have changed at a significantly slower rate than have symbolic traits. This lower rate of turnover, taken at face value, suggests that the functional elements of canoe design were subject to a regime of negative (purifying) selective pressure on the whole, presumably through differential fishing yields, migration success, or survival of the canoe's occupants.

By contrast, the symbolic canoe design traits appear to have evolved more rapidly. Theoretical models of cultural evolution indicate that group differentiation proceeds, at least in part, because of relatively higher within-group and lower between-group transmission coefficients (6). Anthropologists and sociologists have long noted a human tendency to generate and reinforce ethnic identity by using, among other things, a variety of symbolic markers (31–34). These tendencies appear to have driven a more rapid turnover of symbolic traits in Polynesian canoes, possibly through intentional cultural selection of traits to differentiate the cultures from one another.

The slower rate of change of functional canoe design traits could also reflect cultural selection. Although cultural selection and natural selection have been shown to operate at cross-purposes on occasion (8, 35–37), there is no reason to suspect such a case here. If anything, cultural choices would work in tandem with natural selection, because people would have been careful to retain effective canoe designs. This retention is especially important for small populations, which are highly subject to loss of traits through drift. As pointed out by Shennan (38), any cultural attribute maintained by a small population in the face of drift suggests that either strong measures are being taken to retain it, or it is conferring strong selective advantage. It is interesting to note that canoe-building knowledge in Oceania is rapidly eroding now that it is no longer essential to survival (39).

What do these results suggest about cultural evolution? First and foremost, they support interpreting cultural change from an evolutionary perspective by demonstrating a theoretically based pattern (i.e., that characters tested against the environment evolve at a different rate) that could be used to understand or predict cultural change in other instances. This finding does not mean that cultural change comes about through genetic evolution. It simply means that despite the different ways in which cultural traits are transmitted, predictable evolutionary mechanisms may contribute to resulting patterns of change.

Second, our results help to untangle the relationships between cultural change and the different selective forces that might act on it systematically. If cultural traits that could affect survival and reproduction (e.g., through colonization, fishing, or warfare) evolve at a significantly different rate from cultural traits that do not, then this lends support to the distinction and its operational consequences. Again, this does not imply that genetic change causes differentiation of cultural types. In fact, the causal relationship may be reversed, with selection on cultural traits leading to different survival and reproduction outcomes for individuals or populations involved. Given two relatively small island populations in which founder effect and drift have led to differences in gene frequencies, individuals of one population may experience a significant reproductive advantage if their fishing expeditions or colonization voyages to found new settlements are more successful because of better canoe design.

Third, the observation that canoe design elements with potential fitness consequences experienced slower rates of evolution, possibly because of negative (purifying) selection, suggests that canoe designs do not benefit from random innovations but change conservatively, perhaps based on changes that are carefully chosen by people to increase the functionality of the canoes.

In concrete terms, functional canoe designs may well have played a role in the success or failure of oceanic migrations, fishing trips, and warfare (40). Simulation models of human survival on oceanic canoe voyages (41–45), Polynesian oral histories, historical records and information about prehistoric conditions (45–48), and contemporary experiences of sailing replicas (49–51) indicate a substantial probability of death, linked in part to canoe design, on such trips. Although we tend to think of Polynesia as a comfortable tropical environment, experience, weather records, and simulations indicate the very real danger of death from hypothermia due to exposure to wet, windy conditions on long canoe voyages (45). Voyage success or failure, in turn, would have had consequences for the survival, migration, and reproduction of the people involved and thus for the promulgation of canoe designs or even entire cultures.

Rates of evolution, whether genetic or cultural, appear to be affected by selection regimes. With models indicating voyaging-related mortality potentially on the order of 50% (41, 45), favorable canoe design traits should experience turnover only when new design traits were equally or more beneficial. This process is a powerful and systematic selective force, having consequences for the cultures of the survivors' descendants and possibly for their genes, as well. Future research directions suggested by this finding include comparing clusters of canoe design traits for discernable patterns in rate of evolution, breaking down trait distances into rates of trait loss and innovation to investigate the role of random drift in the evolution of these traits, using multimodel inference to explore the potential contributions of drift, cultural selection, and natural selection, and, most important, developing a variety of different cultural data sets on which to run similar analyses.

Methods

Presence/Absence Data Matrix. A data matrix consisting of presence/absence data for canoe design features for outrigger and double hull canoes was created for various Polynesian island groups. Characteristics of Polynesian canoe design and construction were obtained from Haddon and Hornell (1936–1938) (30). This three-volume source presents descriptions of traditional canoe design for cultures from each island or island group (archipelago) in Oceania. Haddon and Hornell's descriptions were gleaned from records left by early European explorers and from original canoes and miniature replicas found in museums around the world. The text distinguishes between traditional canoe designs (which we used) and designs influenced by later contact with Asian and European cultures (which we did not use). The traits we coded were a combination of functional canoe design traits listed as "salient" by Haddon and Hornell (ref. 30, Vol I, p 441), other functional traits mentioned frequently, and symbolic (aesthetic, social, or spiritual) canoe decorations described in their text.

A data matrix consisting of presence/absence data for these canoe design features was created for 11 island groups. Each description provided by Haddon and Hornell was coded into the appropriate island group-by-canoe trait cell as a presence value, 1, or absence value, 0. Island groups and canoe types for which the data were not complete were not used in the data matrix. All traits were organized under two main canoe type headings: outrigger canoes and double-hull canoes.

Next, clusters of traits that were not independent were identified, and traits providing redundant information were removed. A trait-by-trait correlation matrix was developed to assist in identifying clusters of related traits (52). Clusters of traits with a correlation coefficient of >0.7 were identified, and 18 traits that appeared to provide redundant information were removed. This was done to avoid unduly weighting any particular types of traits. (Note that the remainder of the analysis was conducted both before and after the removal of these traits, and this process did not substantially alter any results.) The final data matrix, then, had 11 island groups (see [SI Table 1](#)) and presence/absence data for 134 design traits (96 functional and 38 symbolic; see [SI Table](#)

2). The complete 11×134 matrix of presence/absence data is presented in [SI Table 3](#).

Jaccard Distance Matrices. Island-by-island cultural distance matrices were created from the presence/absence data by using a Jaccard distance measure (number of dissimilar traits in two-island pair)/(total number of traits in two-island pair). This process normalizes differences in the fraction of traits present (out of the total trait set), allowing us to make fair comparisons between categories of traits that are very different in their behavior (see [SI Methods](#) for a complete rationale). Use of the Jaccard distance, which ignores shared absences, is appropriate when comparing relative rates of change because shared absences often reflect changes that did not take place between the two islands for which the distance is being calculated. Three Jaccard distance matrices were generated: one based on the functional traits only, one based on the symbolic traits only, and one based on the functional and symbolic traits combined.

Mantel Test. A two-way Mantel test (53, 54) was used to determine the extent of correlation in patterns of change between the functional and symbolic canoe design traits. This test is designed to look for association between two dissimilarity matrices, given that there will be internal correlations within each matrix. (Note that these internal correlations are an outcome of the island-by-island matrix structure and are not related to the problem of internal correlations in the raw data mentioned earlier.) The Mantel test works by multiplying matching cells in the two distance matrices and then summing these products to generate a Z statistic. When larger values cooccur, the Z-value will be larger. The Z-value is meaningless until normalized in some fashion, because its absolute magnitude is a function of the specific values in the two matrices. It is normalized by running the same set of calculations on a number of randomly generated matrices, bootstrapped several hundred to several thousand times. Our Mantel test was performed by using the MXCOMP program in James Rohlf's NTSYS-pc numerical taxonomy package (1,000 iterations). The normalized Z value (r) was 0.00108, and the P value was 0.5029. From this, we conclude that there was a very small and insignificant association between the functional and symbolic distance matrices.

Sign Test. To compare the functional and symbolic trait distance matrices for relative rates of divergence, we used the Sign test (54), a very simple non-parametric test for differences between two groups of paired observations. Parametric statistical tests are predicated on the assumptions of independence and normality, neither of which is met here. But, what about nonparametric tests like the Sign test? If independence is not necessary for nonparametric tests to be valid, then several such tests (two-tailed) we ran in MatLab show that the two matrices are significantly different: the Sign test (see above), the Wilcoxon signed rank test ($P = 1.3597 \times 10^{-7}$), the Mann-Whitney or Wilcoxon rank sum test ($P = 1.0177 \times 10^{-12}$), and the Kolmogorov-Smirnov test (reject null hypothesis; P value not provided by MatLab).

However, if the internal correlations inherent to a distance matrix invalidate these tests, then we need to run a permutation or randomization and calculate the probability of achieving some relevant test statistic value in the context of distance matrices. Such a randomization must preserve the structure and internal correlations of the matrices, must be based on some relevant test statistic that is designed to distinguish between paired samples that are not normally distributed, and must be permuted or randomized a sufficient number of times to generate a reliable probability distribution of the test statistic against which to compare the value of the test statistic for the actual data set.

Wilcoxon Signed Ranks Randomization. A permutation test (55) was developed that meets the above criteria. A randomization was performed on the choice of traits assigned as functional or symbolic. Traits were randomly assigned to the categories (but in the same ratio of 96 functional to 38 symbolic) for 10,000 iterations (programmed in Java). The resulting bootstrapped data sets were then analyzed by creating the two Jaccard distance matrices[†] (one for each type of trait) and running the Wilcoxon signed ranks test (54) on each pair of matrices. This is another common nonparametric test for differences between two groups of paired observations. A frequency distribution of the resulting Wilcoxon test statistics was plotted (see [SI Fig. 4](#)). Although the probability of obtaining the test statistic calculated by using this randomization was not as

[†]Lee L (1999) Measures of distributional similarity. *37th Annual Meeting of the Association for Computational Linguistics* (Association for Computational Linguistics, College Park, MD), pp 25–32.

extreme as the *P* value generated by the Sign test, it still supports the conclusion of significance.

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