

Cultural assemblages show nested structure in humans and chimpanzees but not orangutans

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The evolution of hominin culture is well-documented in the archeological and fossil record, but such a record is largely absent for nonhuman primates. An alternative approach to studying cultural evolution is to examine patterns of modern cultural variation. In this article we measure nestedness across human and great ape “cultural repertoires” to gain insight into the accumulation and maintenance of putative cultural diversity in these species. Cultural assemblages are nested if cultures with a small repertoire of traits tend to comprise a proper subset of those traits present in more complex cultures. This nesting will occur if some traits are sequentially gained or lost, which may be because of the differential dispersal or extinction of traits. Here we apply statistical tools from ecology to examine the degree of nestedness in four datasets documenting the presence or absence of specific cultural traits across indigenous human populations in North America and New Guinea. We then compare the human data to patterns observed for putative cultural traits in chimpanzee and orangutan populations. In both humans and chimpanzees, cultural diversity is highly nonrandom, showing significant nested structure for all of the datasets examined. We find no evidence for nestedness in the orangutan cultural data. These findings are consistent with a sequential “layering” of cultural diversity in humans and chimpanzees, but not orangutans. Such an interpretation implies that the traits required for sequential cultural evolution first appeared in the last common ancestor of chimpanzees and humans.

behavior | geographic variation | biogeography | tool use | socially transmitted

In recent years, biologists and anthropologists have been particularly interested in across-site behavioral variation in humans and nonhuman animals that is potentially cultural in nature. The discovery in many species of distinct behavioral traditions across populations that are not obviously attributable to genetic or ecological differences supports the existence of socially transmitted information or “culture” in nonhuman animals (1–14). However, relatively little work has been done to quantify variation of socially transmitted behaviors in a comparative context (but see refs. 15 and 16). There remain disagreements about the extent to which animal traditions differ from human culture in complexity, how complexity varies through time and space (17), and the capacity for a “ratchet effect” (18, 19) or cumulative cultural evolution (20).

Some of the best-documented evidence for culture in nonhumans comes from detailed records of the frequency of specific behaviors in wild populations of chimpanzees (1, 2) and orangutans (3, 4). These behavioral repertoires closely resemble databases developed by anthropologists to record cultural variation between human populations (21–23). This similarity creates the opportunity to compare macroscale patterns of across-site cultural variation between humans and our closest primate relatives, providing insight into the evolution of culture and the human capacity for culture (24, 25). For example, if patterns of cultural diversity in humans and chimpanzees are similar, then this suggests these patterns were also present in the last common ancestor of these species.

Recent research comparing the cultural diversity of humans and chimpanzees has often yielded conflicting and sometimes contentious results. A recent report by Lycett et al. (16) applied phylogenetic methods to human and chimpanzee cultural datasets and found that they exhibited similar degrees of tree-like (i.e., hierarchical) structure. The authors’ findings suggest that the basic mechanisms producing cultural diversity in these species may be similar. Other studies have examined the relative importance of geography, genetics, and local ecology for explaining geographic variation in cultural repertoires. For humans and chimpanzees, cultural repertoires are more similar among localities that are in close proximity to each other, with little influence of ecological factors (22, 26). These results are commonly interpreted as resulting from the innovation and diffusion of cultural traits across study sites [although, see Langergraber et al. (27) for a possible genetic mechanism for chimpanzees]. Interestingly, Krützen et al. (12) found that neither environmental variation nor genetics (i.e., geography) were good predictors of orangutan behavioral variation across sites.

Here we use a unique application of an analytical technique that quantifies additional aspects of the hierarchical structure of cultural repertoires. This approach, adapted from macrolevel analyses of community ecology, quantifies the nestedness (i.e., hierarchical structure) of datasets. Across-site variation in species assemblages is highly nonrandom (28–34) and often shows a nested pattern, such that sites with lower species richness tend to comprise a proper subset of species at richer sites (35–39) (Fig. 1). These patterns give ecologists insight into how ecosystems evolve, the process of ecological succession, and the relative importance of individual species to ecosystem diversity (35). We

Significance

The evolution of culture is well-documented in the human archeological and fossil records, but equivalent data are absent for nonhuman primates. Here, we use modern variation to learn about processes of temporal evolution by measuring nestedness across human and great ape “cultural repertoires.” Cultural assemblages are nested if cultures with a small repertoire of traits tend to comprise a proper subset of traits present in more complex cultures. We find a significant degree of nestedness in human and chimpanzee cultural repertoires, but not for orangutans. Our findings are consistent with a sequential “layering” of culture in humans and chimpanzees only, suggesting that the traits required for sequential cultural evolution first appeared in the last common ancestor of these species.

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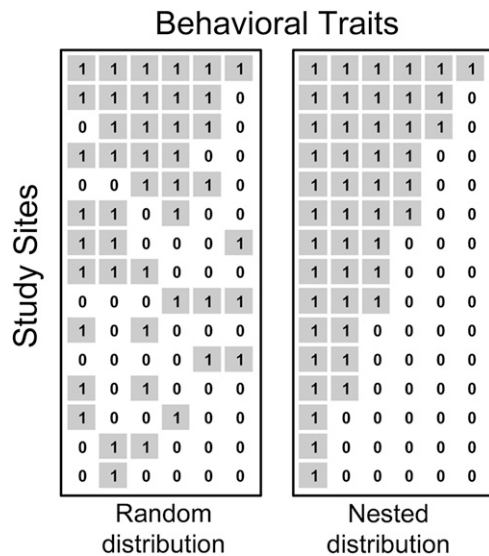


Fig. 1. Examples of random (Left) and significant (Right) patterns of nestedness. Traits are represented by columns and study sites are represented by rows. Shaded cells with a value of 1 indicate the presence of a trait at a site. Unshaded cells with a value of 0 indicate the absence of a trait at a site. Modified from Almeida-Neto et al. (38).

apply the same nestedness metrics to answer analogous questions about across-site variation of behavioral repertoires in humans, chimpanzees, and orangutans. For each species, we test whether putative cultural traits show a random distribution between populations or a nested structure.

Nested cultural variation may result from several different scenarios that are similarly observed in the geographic variation of ecological community structure (35, 37). Sequential cultural evolution, analogous to ecological succession, can generate nestedness via the preferential gain of some features in sequence; for example, if some traits are more likely to be invented or borrowed in the presence of others. This process can occur if some traits increase the likelihood of others being subsequently adopted, or if some traits are ubiquitous because they spread easily, whereas others that spread less easily are less likely to be found at increasingly isolated sites. Similarly, nested cultural variation may arise if all variants were originally present at all sites, followed by sequential “extinctions.” For example, some variants may tend to go extinct before others that are especially important to communities, and therefore remain present at most sites. Nestedness may also arise because of a relationship between habitat structure and the presence or absence of specific cultural variants. If the habitats themselves exhibit nested features, this could produce a nested pattern of cultural variation. There is, however, disagreement about the cultural nature of behavioral traits that vary with ecology (40, 41).

A sequential process of cultural change, such that the presence of some traits is contingent on the presence of others, is a likely first step toward a capacity for cumulative cultural evolution and the associated ratchet effect (18). The ratchet effect involves an innovation (or borrowing) spreading through a population of social learners who are then able to innovate in ways that would not have otherwise been possible, moving the ratchet up a notch. Such a process can generate increasingly complex cultural traits (cumulative cultural evolution) but minimally requires that some traits affect the probability of others occurring, whether or not complexity increases.

Cumulative cultural evolution is often suggested to be a unique aspect of human culture (20), but quantifying similar aspects of cultural diversity for nonhumans is challenging because their

behavior is not well preserved in the archeological or fossil records. Here we search for evidence of sequential cultural evolution in the form of cultural nestedness, thereby allowing a comparison between humans and nonhumans. To the extent that nestedness tracks sequential cultural evolution, we expect to find that human cultural repertoires exhibit significantly nested patterns of diversity. Indeed, humans may be the only species exhibiting nested cultural evolution as a result of the unique qualities of their culture (e.g., ratchet effect, extreme cultural diversity and complexity). A lack of nestedness in the cultural repertoires of chimpanzees or orangutans would suggest the absence of processes of sequential evolution. Alternatively, significant cultural nestedness in chimpanzees or orangutans leaves open the possibility of an earlier evolutionary appearance of sequential cultural evolution.

Results

We found strong support for the idea that humans and chimpanzees exhibit a significant amount of nestedness in their cultural repertoires across sites, yet did not find this pattern for orangutans (Fig. 2 and Table 1). The human and chimpanzee datasets show highly significant nestedness for all metrics. In fact, these datasets yielded the lowest possible *P* values based on randomly generated datasets in all but one case. The human datasets display matrix temperatures ranging from a low of 27.48 (Californian Indian) to a high of 40.66 (Western North American Indian). Matrix temperature measures the degree of departure from perfect nestedness, such that higher values indicate increasingly random data. The chimpanzee dataset yielded a matrix temperature within the human range, with values of 31.81–36.51 (depending on the dataset’s coding scheme). The chimpanzee dataset consistently showed a significant amount of nestedness, regardless of the particular coding scheme we implemented.

Based on the NODF(ER) measure (NODF is an acronym for a nestedness metric based on overlap and decreasing fill), one version of the orangutan dataset approaches statistical significance ($P = 0.06$), but this metric does not account for differences in row and column totals, which can artificially inflate

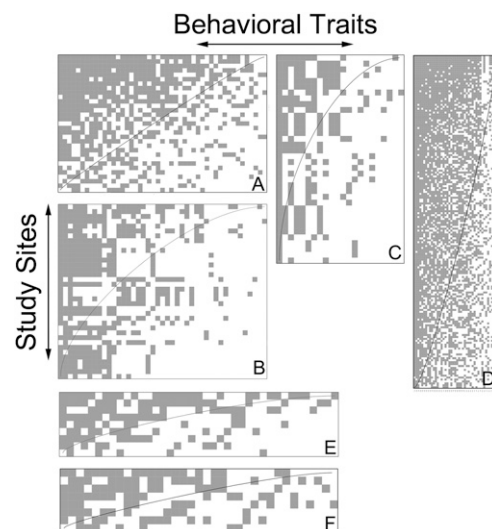


Fig. 2. Site by cultural trait matrices visually representing the degree of cultural nestedness in human (A–D), chimpanzee (E), and orangutan (F) datasets. Shaded cells indicate the presence of a cultural trait at a site. Data were obtained from: (A) Welsch et al. (21), (B) Jordan and Shennan (22) (Types and Uses dataset), (C) Jordan and Shennan (22) (Ornamentation dataset), (D) Jorgensen (23), (E) Whiten et al. (1), and (F) van Schaik et al. (4).

Table 1. Results of NODF and matrix temperature analyses quantifying the degree of nestedness in cultural assemblages

Dataset	NODF (ER)	<i>P</i> value (ER)	NODF (CE)	<i>P</i> value (CE)	Matrix temperature	Temperature <i>P</i> value	% Matrix fill	<i>n</i> sites	<i>n</i> traits
Human: New Guinea (21)	47.00	<0.01	53.03	<0.01	36.10	0.001	46.60	31	47
Human: Californian Indian* (22)	30.32	<0.01	37.32	<0.01	35.90	0.001	31.50	39	43
Human: Californian Indian† (22)	26.72	<0.01	33.68	<0.01	27.48	0.001	27.20	39	22
Human: Western North American Indian (23)	57.31	<0.01	61.16	<0.01	40.66	0.001	58.10	172	43
Chimpanzee‡ (1)	38.64	<0.01	43.20	<0.01	32.46	0.001	36.70	9	39
Chimpanzee§ (1)	49.93	<0.01	55.03	<0.01	31.81	0.001	49.80	9	39
Chimpanzee¶ (1)	30.99	<0.01	34.62	0.03	36.51	0.023	28.40	9	39
Orangutan‡ (4)	42.30	0.06	45.44	0.23	45.15	0.158	40.70	8	35
Orangutan§ (4)	46.49	0.16	49.68	0.47	51.39	0.470	45.70	8	35
Orangutan¶ (4)	25.04	0.29	27.21	0.51	42.87	0.580	22.80	8	35

*Types and uses dataset.

†Ornamentation dataset.

‡Unknown traits coded as absent.

§Unknown traits coded as present.

¶Only habitual and customary traits coded as present.

nestedness scores. Both NODF(CE), which accounts for differences in row and column totals, and matrix temperature indicate the orangutan data are not significantly more nested than random data (Table 1). In addition, orangutans exhibit the highest matrix temperatures of any dataset, with values of 42.87–51.39 (depending on the coding scheme of the traits). The orangutan dataset never exhibited a statistically significant degree of nestedness, regardless of the coding scheme we implemented or the nestedness metric used.

Discussion

We show that geographic variation in human and chimpanzee cultural repertoires are nested, displaying a significant amount of hierarchical structure. In contrast, orangutan cultural diversity does not significantly differ from random. Previous cross-cultural analyses suggest that the nestedness we observe in human and chimpanzee culture is unlikely to be solely the product of covariation with nested ecological features. Jordan and Shennan (22) examined the relative importance of geography and local ecology for predicting the frequency of cultural traits at numerous Californian Indian sites. The authors found that geographic distance between locales was the most important factor driving cultural variation, with little effect of ecology. A recent report examining chimpanzee cultural variation (26) found similar results. Proxies for local habitat conditions, such as rainfall and temperature, were not significant predictors of cultural variation across chimpanzee study sites. In contrast, chimpanzees at sites that were in close proximity to each other displayed more similar cultural repertoires, compared with those living at more distant locales. Therefore, like human culture, chimpanzee culture shows evidence of dispersal via cultural diffusion or processes of descent and expansion. We cannot completely exclude a genetic mechanism for the geographic effect on chimpanzee cultural diversity (27); however, the importance of genetics for driving intercommunity variation in chimpanzee behavior is currently contested (e.g., ref. 42).

Taken together, these results suggest that cultural nestedness in humans and chimpanzees emerges via processes internal to the cultural system, rather than because of nested ecological features. If this is the case, the nested patterns we observe likely reflect a sequential layering (or peeling away) of cultural variants through time. This result is consistent with comparative phylogenetic analyses (16) that have found measures of phylogenetic tree structure in chimpanzee cultural data to fall within the range of human cultural datasets. The concordance of our results is particularly interesting, because Lycett et al. (16) measured different

types of hierarchical structure in the datasets, which reflect phylogenetic transmission of cultural traits. Strictly phylogenetic transmission will not generate nested data if traits are gained and lost independently along the branches of the phylogeny. The patterns of cultural diversity we quantified with our models suggest a different process that could be the result of horizontal or vertical cultural transmission in which the emergence of one trait is contingent on the presence of other traits.

Orangutans appear similar to chimpanzees in terms of the types of behaviors deemed cultural (1, 3). Previous work (12) has shown that neither genetics nor environmental factors strongly predict putatively cultural traits in orangutans, supporting the contention that these behaviors are socially learned. However, the orangutan cultural data do not show a pattern of nestedness. This finding highlights what may be a fundamental difference between the nature of orangutan and human or chimpanzee culture. However, there remain several alternative explanations for the lack of nestedness in orangutan culture. First, the orangutan data have the fewest sites and may therefore be too small for our methods to detect cultural nestedness. We think this explanation is unlikely because the metrics we use are robust to variation in matrix size and shape (38) and the orangutan dataset is only slightly smaller than for chimpanzees (8 sites and 35 traits vs. 9 sites and 39 traits, respectively). Matrix fill has also been shown to influence temperature scores (38), but the orangutan data are within the range of variation for the chimpanzee datasets. A second possible explanation is that orangutans across Borneo and Sumatra are consistently found in rainforest habitats. This finding is in contrast to the more heterogeneous environmental conditions that chimpanzees occupy, ranging from rainforest to dry forest to savanna (26, 44, 45). Therefore, the relatively uniform habitats that orangutans occupy may reduce the need for different cultural repertoires. Third, the current geographic range of orangutans is relatively small and fragmented, only being found in northern Sumatra and Borneo (46). This range is in stark contrast to their distribution during the Late Quaternary. During this time, there is evidence for orangutans inhabiting Java, Thailand, Laos, Cambodia, Vietnam, and China (47). The widespread population level extinctions of orangutans may have been associated with the substantial extinction of many cultural traits in a nonordered fashion, producing a nonnested pattern of cultural traits in extant orangutan populations. Previous authors (16) have suggested that significant demographic shifts have resulted in the loss of cultural traits in some chimpanzee populations. We would argue that this may have occurred to an even greater extent in orangutans. Finally, orangutans exhibit a relatively dispersed and

less gregarious social organization compared with humans and chimpanzees. Consequently, the reduced sociality of orangutans may lead to distinct patterns of cultural diversity. In particular, orangutan social organization may provide fewer opportunities for social learning (15), which may translate into nonnested cultural repertoires at the interpopulation level.

Our results may also have implications for the conservation of culture. Although animal conservation is most focused on preserving genetic diversity, preserving the cultural diversity of humans, and species such as cetaceans and nonhuman primates, is also essential (48). Ecologists have used species nestedness to show that one large population is often better than many small ones in the same area (35). Cultural nestedness suggests the same logic may apply to culture. When cultural diversity is lost across sites (perhaps because of population loss or habitat loss), then not only will any one population have low cultural diversity, but current cultural diversity across all such extant populations is likely to represent a much reduced subset of former cultural variation. This finding could have important implications for understanding and maintaining cultural diversity in populations (human and chimpanzee) that have undergone fragmentation or population collapse.

Our unique application of nestedness analysis enables us to test for a signal of sequential evolution in human cultural variation across sites. We found a similar pattern of cultural variation in chimpanzees, but not in orangutans. To the extent that these patterns reflect an underlying capacity for the sequential adoption of cultural traits through time and space, our result indicates that such a capacity may have evolved in the last common ancestor of chimpanzees and humans. Alternatively, orangutans may share this cognitive architecture, but have recently lost this aspect of their cultural diversity because of widespread population-level extinctions during the Quaternary. Future research on cultural nestedness should investigate the extent to which these patterns hold across other species, examine possible differences between types of cultural traits, such as material versus gestural culture, and identify the specific features of cultural transmission required to produce nested cultural repertoires.

Materials and Methods

Data Collection. We used six published datasets that quantified geographic variation in cultural traits: four human, one chimpanzee, and one orangutan (Dataset S1). Our first human dataset was obtained from Welsch et al. (21). The authors quantified 47 traits across 31 villages throughout the north coast of New Guinea. Each trait was an "object class" (e.g., nose ornaments, earthenware, bows, and so forth), which represented the material culture at a site. The frequency of specimens for each object class was recorded for each site based on museum collections. Our second human dataset was obtained from Jordan and Shennan's (22) publication on the basketry traditions of Californian Indians. We used data from two of their tables, one that quantified basketry types and uses and the other on basketry ornamentation. This study contained data from 39 sites, and included 43 traits for the former and 22 traits for the latter. Our final human dataset was obtained from Jorgensen (23). These data code the presence or absence of Jorgensen's (23) technological traits related to clothing, housing, and subsistence activities at western North American Indian tribal sites, comprising 43 traits across 172 sites. Approximately 1.4% of the cells in this trait by site data matrix were coded as unknown by the original authors. To maximize our sample size and test for data sensitivity, we conducted two sets of analyses, one coding unknowns as absent and the second coding unknowns as present. The results of these analyses were nearly identical. Therefore, we only present the results with unknown trait by site cells coded as absent.

For chimpanzees, we used the previously published dataset from Whiten et al. (1) (table 3 in ref. 1), including an updated quantification of one trait from the Tai site, which is presented in Langergraber et al. (27). This dataset contained 39 cultural traits that varied across sites and were quantified from eight locations representing nine different communities where previous examinations of between-population variation in behavior have been conducted. These data were deemed putative cultural traits because they varied in frequency across study sites and are believed to be unrelated to local

ecological conditions, although the latter criterion was not tested in the original paper (1). Whiten et al. (1) created an ordinal scale for the frequency of the behavior at each site, from least to most frequent: absent, present but nonhabitual or customary, habitual, and customary. Some traits, especially at Assirik and Lope, were coded as unknown. Therefore, we created two versions of this dataset, one coding all unknowns as present, and the other coding all unknowns as absent. This approach was recently used by Kamilar and Marshack (26). In addition, we treated the original dataset in a third fashion, by only considering habitual and customary traits as present, and all other frequencies as absent. Using three coding schemes allowed us to test the sensitivity of our results to variation in trait frequency. We present the results of our analyses using all coding schemes, although they are qualitatively similar. We used van Schaik et al. (4) for the basis of our orangutan data. This study recorded 35 cultural traits across eight study sites throughout Borneo and Sumatra. Cultural traits were quantified in the same fashion as the Whiten et al. (1) study. In addition, one site, Kutai, contained some traits that were of unknown frequency. We implemented three coding schemes for the orangutan dataset in a similar fashion to the chimpanzee data. It is important to note that the chimpanzee and orangutan datasets comprised cultural traits that were both material and gestural in nature. For example, in chimpanzees several traits were related to food acquisition and processing tools, such as "nut-hammer" and "ant-fish." Other cultural traits have some social function, such as "knuckle-knock" and "hand-clasp."

Data Analyses. We used two methods to calculate the degree of nestedness in behavioral repertoires. Implementing these varied approaches allows us to be more confident that our results are not the product of the way we quantified nestedness or the method of randomization to generate P values. First, we used Atmar and Patterson's (35) NestCalc software to measure the degree of nestedness in our data. This metric calculates a system's "temperature." Temperature is measured for each behavior and site. These temperatures, in turn, are used to calculate the overall temperature of the dataset. A temperature of 0 equates to a perfectly nested dataset, with nestedness decreasing as the temperature of the dataset increases. We performed 999 randomizations of the original dataset to determine if the dataset was more nested than expected by chance alone. Although this method has been the most commonly used approach in community ecology, it has received some recent criticisms (49). Almeida-Neto et al. (38) demonstrated that the temperature metric is sensitive to both matrix size and shape. Because our datasets vary in matrix size and shape, we also used a recently developed method that tests for the amount of nestedness in a dataset, yet is not sensitive to these matrix characteristics. Almeida-Neto et al.'s (38) nestedness metric, NODF, is an acronym for nestedness metric based on overlap and decreasing fill. We used the ANINHADO software package (38, 50) to calculate the NODF metric for each dataset. We used two randomization models to calculate statistical significance. The simple model (ER) tests against the random assignment of presences to any cell in the data matrix. The second model (CE) is more discerning, with the probability of a cell displaying a presence being dependent on the number of presences in the row and column. The CE model allows us to test whether the level of observed nestedness is more than we would expect, given that some traits are more common than others and some sites have higher diversity than others. We used 999 randomizations to generate P values, although the software's output only reports two decimal places.

Both methods only accept binary data, yet our datasets were originally measured as ordinal or frequency variables. Therefore, we converted the original data into two categories: "0" for traits that were absent and "1" for traits that were present at a site, as long as they occurred at a rate or frequency greater than zero (with some exceptions; see *Data Collection* section for more details).

The software packages maximally pack the data matrix to best approximate an ideally nested pattern. In a perfectly nested matrix the topmost row (i.e., study site) has all behaviors present, and the bottommost row has the fewest (see Fig. 1 for example). The leftmost trait is assumed to be the most common, defined as being present in most sites. Similarly, the rightmost trait is the rarest, defined as being present in the fewest communities (See Dataset S1 for data matrices).

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