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Behavioural variation in 172 small-scale societies indicates that social learning is the main mode of human adaptation

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The behavioural variation among human societies is vast and unmatched in the animal world. It is unclear whether this variation is due to variation in the ecological environment or to differences in cultural traditions. Underlying this debate is a more fundamental question: is the richness of humans' behavioural repertoire due to non-cultural mechanisms, such as causal reasoning, inventiveness, reaction norms, trial-and-error learning and evoked culture, or is it due to the population-level dynamics of cultural transmission? Here, we measure the relative contribution of environment and cultural history in explaining the behavioural variation of 172 Native American tribes at the time of European contact. We find that the effect of cultural history is typically larger than that of environment. Behaviours also persist over millennia within cultural lineages. This indicates that human behaviour is not predominantly determined by single-generation adaptive responses, contra theories that emphasize non-cultural mechanisms as determinants of human behaviour. Rather, the main mode of human adaptation is social learning mechanisms that operate over multiple generations.

1. Introduction

People in different societies eat different foods, use different technologies, follow different marriage practices and believe in different gods. This behavioural diversity is unmatched in the animal world [1] and is rivalled only by the behavioural variation found between different species. For over a century, scholars have debated where this behavioural diversity comes from [2–5]. On the one hand, our unique behavioural diversity could come from the unusually wide range of environments we inhabit. On the other hand, it could also be due to differences in cultural traditions, caused by our unprecedented reliance on social learning. Underlying this debate is a more fundamental question: is the richness of our behavioural repertoire due to non-cultural mechanisms, such as causal reasoning, inventiveness, reaction norms, trial-and-error learning and evoked culture, or is it due to the population-level dynamics of cultural transmission [6–11]?

Different ecological environments can give rise to behavioural differences among human societies [8,12–15]. Environments can undoubtedly constrain behaviour—one cannot fish in the desert. In addition, individuals can adjust their behaviour to local environments through various mechanisms. For instance, humans, the most encephalized species on the planet, can use causal reasoning and inventiveness to create solutions to ecological problems, a mechanism that is at the centre of the cognitive niche hypothesis [16]. Behavioural flexibility also allows individuals to respond to their environment in adaptive ways, whether through trial-and-error learning, rational choice decision-making or reaction norms, as emphasized in human behavioural ecology [12,17–20]. In addition, humans have domain-specific cognitive modules that elicit different behaviours in response to different ecological input, a phenomenon referred to as evoked culture and put forward by evolutionary psychologists [7,14]. In addition to these mechanisms, social learning can also lead to behaviours that are adapted to local environments [6,21,22]. However, with the exception of social learning, all these mechanisms exclusively operate within a single generation.

Cultural history can also lead to behavioural variation between groups [3,15,23–28]. Behaviours can be socially transmitted between members of neighbouring groups. This causes groups that are located close to one another to be more behaviourally similar than groups that are farther apart [29]. Behaviours can also be socially transmitted between members of the same group, causing behaviours to persist over multiple generations within a cultural lineage. This means that between-group behavioural variation can be due to the phylogenetic history of cultural lineages rather than variation in contemporary environments.

Here, we compare the relative effect of environment and cultural history in explaining the behavioural variation across 172 tribes in western North America at the time of European contact. We estimated the probability that a tribe possesses a behavioural trait based on its ecology and its cultural history. Cultural history was partitioned into two components: cultural phylogeny (to capture transmission within cultural lineages) and spatial distance to other tribes (to capture diffusion between groups).

We used the Western North American Indian (WNAI) dataset [4,30], one of the most comprehensive ethnographic records of small-scale societies. This dataset is unique for the large number of foraging societies it contains—127 of the 172 tribes relied exclusively on hunting and gathering for acquiring their food, and only 16 of them relied mostly on agriculture. The dataset contains information on 297 behavioural traits spanning the gamut of human behaviours: technology and material culture, subsistence, economic organization, settlement pattern, marriage and family organization, kinship system, political organization, sodalities, warfare, ceremonies and rituals, and supernatural beliefs. The dataset is also unique for its ecological breadth. The tribes are distributed across 30° of latitude, 40° of longitude, and 8000 feet of altitude, and their habitats include various types of desert, grassland, forest and tundra. The environment the tribes live in is described by 133 variables, including altitude, temperature, precipitation and the presence of 125 species of plants and animals. The tribes also have different cultural histories, as evidenced by the fact that they speak 116 distinct languages.

Our analysis augments previous efforts at measuring the importance of ecology and cultural history in shaping human behaviour. Several studies have examined the extent to which behavioural traits are transmitted within or between groups, but without considering the effect of ecology [26,28,31–33]. Other studies have considered the effect of ecology and cultural history, but looked only at specific sets of behaviours, such as canoe design [25], religious beliefs [15] or personality traits [3]. The studies that have looked at a broader range of behaviours have found the effect of culture to be larger than that of ecology [23,24]. However, these studies used coarse variables to describe ecology, which could have led them to underestimate the effect of ecology. For instance, Hewlett et al. [23] analysed the behavioural variation among 36 ethnic groups in Africa, but divided the groups into three habitats. Similarly, Guglielmino et al.'s study [24] of 277 societies in sub-Saharan Africa measured the effect of ecology using six types of ecological habitats. Here, we take advantage of the fact that the WNAI dataset includes a wide range of behavioural traits as well as a rich description of ecology to quantify the effect of ecology and cultural history in explaining human behavioural variation.

2. Material and methods

(a) Sampling procedure

The sampling procedure used by the authors of the WNAI dataset was designed to minimize systematic biases that could affect our results. The dataset was originally created to evaluate the respective role of environment and cultural history in explaining behavioural variation between societies [30]. Consequently, it includes a wide array of behavioural traits, which range from traits that may be strongly influenced by cultural history (e.g. importance of the number '3' in rituals) to traits that may be strongly influenced by ecology (e.g. fish as a staple food). To determine which societies to include in the sample (e.g. should two communities that speak the same language and share a common border be treated as one tribe or two tribes?), the authors treated as one tribe the communities that spoke the same language (or different dialects of the same language), shared a common border and shared 80% or more of their behavioural inventories [30]. Because the groups treated as one tribe are similar behaviourally, ecologically and linguistically, and are close spatial neighbours, this procedure does not privilege ecology, cultural phylogeny or spatial distance as a predictor of behavioural variation.

(b) Behavioural variables

The 297 behavioural variables in the WNAI dataset are categorical, with multiple values. We transformed these into present/absent variables, which resulted in 457 behavioural traits. We dropped the behavioural variables that are present in less than 10% of the tribes, because they lack the variation required to fit a logistic regression model. The complete dataset, along with the script and procedure for dichotomizing the variables, can be found in the electronic supplementary material.

(c) Ecological predictors

There are 135 ecological variables in the WNAI dataset. We re-classified one variable (relative amount of fish used as food by a tribe) as a behavioural variable, and eliminated one variable (presence of the plant lambsquarter), as it does not vary between tribes. As a result, we had 133 ecology variables, including altitude, average annual precipitation, average temperature in winter and summer, life zones, vegetation area, as well as the presence of 54 species of plants, 29 species of marine mammals, 19 species of fish, 19 species of land animals and four species of birds. Note that the main domesticated crops in North America (corn, squash, beans, cotton and tobacco) are not classified as ecological variables. Instead, the use of these plants is coded among the behavioural variables.

The ecological variables in the dataset are different from some of the variables that are emphasized in theories linking human behaviour and ecology, such as patchiness and productivity. Our analysis will capture the effect of these emphasized variables to the extent that they correlate with the ecological variables in the dataset. But there are two situations in which our analysis would fail to capture the effect of these emphasized variables: first, if the tribes in our sample live in environments that are similar according to our 133 ecological variables, but differ in, say, patchiness; or second, if the tribes live in environments that are different according to our 133 ecological variables, but that are similarly patchy.

(d) Cultural phylogeny

We used the language phylogeny of the tribes to represent their cultural phylogeny [34]. Specifically, we used Ruhlen's classification of North American languages [35] and measured phylogenetic distance as the number of steps to the most recent common ancestor. Ruhlen's classification comprises 11 hierarchical levels. The deepest level, phylum, splits the 172 tribes in two groups—Na-Dene and Amerind. The most recent level, language, splits the 172 tribes into 116 languages (as some of the tribes speak the same language). The
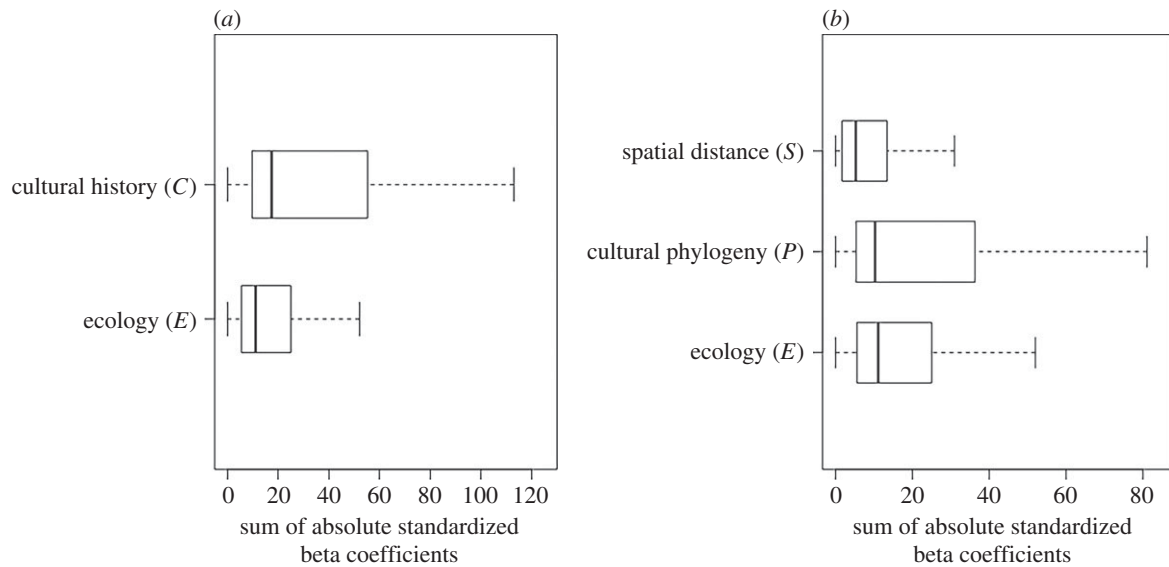
Figure 1. Cultural history has a larger effect than ecology on the presence or absence of traits in a tribe. Boxplots of (*a*) *C* and *E*, and (*b*) *P*, *E* and *S*, for 457 behavioural traits. Boxes show the median, 25th and 75th percentiles, error bars show 1.5 IQD.

three levels that immediately preceded language were not included in our analysis, because data for these levels were missing for more than 75% of the tribes. We labelled the remaining eight levels so that the oldest level (phylum) is Level 1, and the most recent level (language) is Level 8. When tribes have missing values at certain levels, we assumed that they did not share a common ancestor at a more recent level than what is specified in Ruhlen's classification.

We transformed Ruhlen's classification into a linguistic distance matrix. We calculated the linguistic distance between each tribe's language (Level 8) and the other 115 languages. The linguistic distances are the numbers of levels between Level 8 and the levels at which a language shares its most recent common ancestors with the other languages. Thus, the distance between two languages sharing a most recent common ancestor at Level 7 is 1, at Level 6 is 2 and so on. For example, the linguistic distance between the Hualapai and Havasupai languages is 1, because their most recent common ancestor, Upland Yuma, occurs at Level 7. Similarly, the linguistic distance between Hualapai and Yuki languages is 7, because their first common ancestor, Amerind, occurs at Level 1. As there are 172 tribes and 116 languages, the linguistic distance takes the form of a 172×116 matrix. We used this linguistic distance matrix in order to compare the relative effect of ecology, cultural phylogeny and spatial distance (e.g. figures 1 and 2).

To evaluate how long behaviours persist in lineages, we examined how the effect of cultural phylogeny decreases as we pruned down the language phylogeny. To do this, we created seven additional versions of the linguistic distance matrix. The original distance matrix, which we call Time Depth 8, includes all eight levels of the language classification. We created another matrix, which we call Time Depth 7, that contains distances calculated using only the first seven phylogenetic levels (Levels 1 to 7). Thus, in the Time Depth 7 matrix, the linguistic distance is calculated between each tribe's Level 7 category and the other 84 Level 7 categories (resulting in a 172×85 linguistic distance matrix). We repeated this procedure to create a matrix using only the first six phylogenetic levels (Levels 1–6, called Time Depth 6), to create a matrix using only first five phylogenetic levels (Levels 1–5, called Time Depth 5), and so on. Time Depth matrices 1–8 were used to explore how the cultural phylogenetic signal decreases with time (e.g. figure 3).

(e) Spatial distance
To measure spatial distance, we used the latitude and longitude coordinates of the tribes provided in the WNAI dataset. Distances

were calculated between each pair of tribes as the crow flies using the spherical law of cosines. The result is a 172×172 matrix specifying the geographical distance between each pair of tribes.

(f) Statistical analysis
In order to perform an exhaustive search for the best model, we used correspondence analysis methods to reduce the total number of ecology, cultural phylogeny and spatial distance predictors. We retained the minimum number of components that captured at least 93% of the variation of each class of predictors (electronic supplementary material, table S7). We used joint correspondence analysis on the ecology predictors using Stata's *mca* function. We performed principal component analysis on the spatial distance matrix, and six of the linguistic distance matrices, using the *prcomp* function in R. We did not perform PCA on the Time Depth 1 and Time Depth 2 matrices, but used the original variables, as there were only two and four variables for these time depths, respectively.

For each of the 457 behavioural traits, we fitted a logistic regression. For each trait, we fitted every possible combination of ecology, cultural phylogeny and spatial distance predictors, resulting in 131 071 different models per trait. The combinations of predictors were screened with an exhaustive search using the *glmulti* function in the *glmulti* package in R, with no constraints on candidate models, and with no interaction effects. We used the Akaike information criterion (AIC) scores of the models to identify the single best model. Thus for each trait, the probability p that a trait is present is given by

$$\text{logit}(p) = a + \boldsymbol{b}_E \cdot \boldsymbol{z}_E + \boldsymbol{b}_P \cdot \boldsymbol{z}_P + \boldsymbol{b}_S \cdot \boldsymbol{z}_S,$$

where a is the intercept, $\boldsymbol{b}_E$, $\boldsymbol{b}_P$ and $\boldsymbol{b}_S$ are vectors of the coefficients for the ecology, cultural phylogeny and spatial distance predictors, respectively, included in the best model, and $\boldsymbol{z}_E$, $\boldsymbol{z}_P$ and $\boldsymbol{z}_S$ are vectors of the values of the ecology, cultural phylogeny and spatial distance predictors, respectively, included in the best model.

For each trait, we calculated the overall effect of ecology (*E*) and culture (*C*), which is the sum of cultural phylogeny (*P*) and spatial distance (*S*) as

$$E = \sum_{i=1}^{n_e} |\boldsymbol{\beta}_i^E|$$

$$\text{and} \quad C = \underbrace{\sum_{i=1}^{n_P} |\boldsymbol{\beta}_i^P|}_{P} + \underbrace{\sum_{i=1}^{n_s} |\boldsymbol{\beta}_i^S|}_{S}$$

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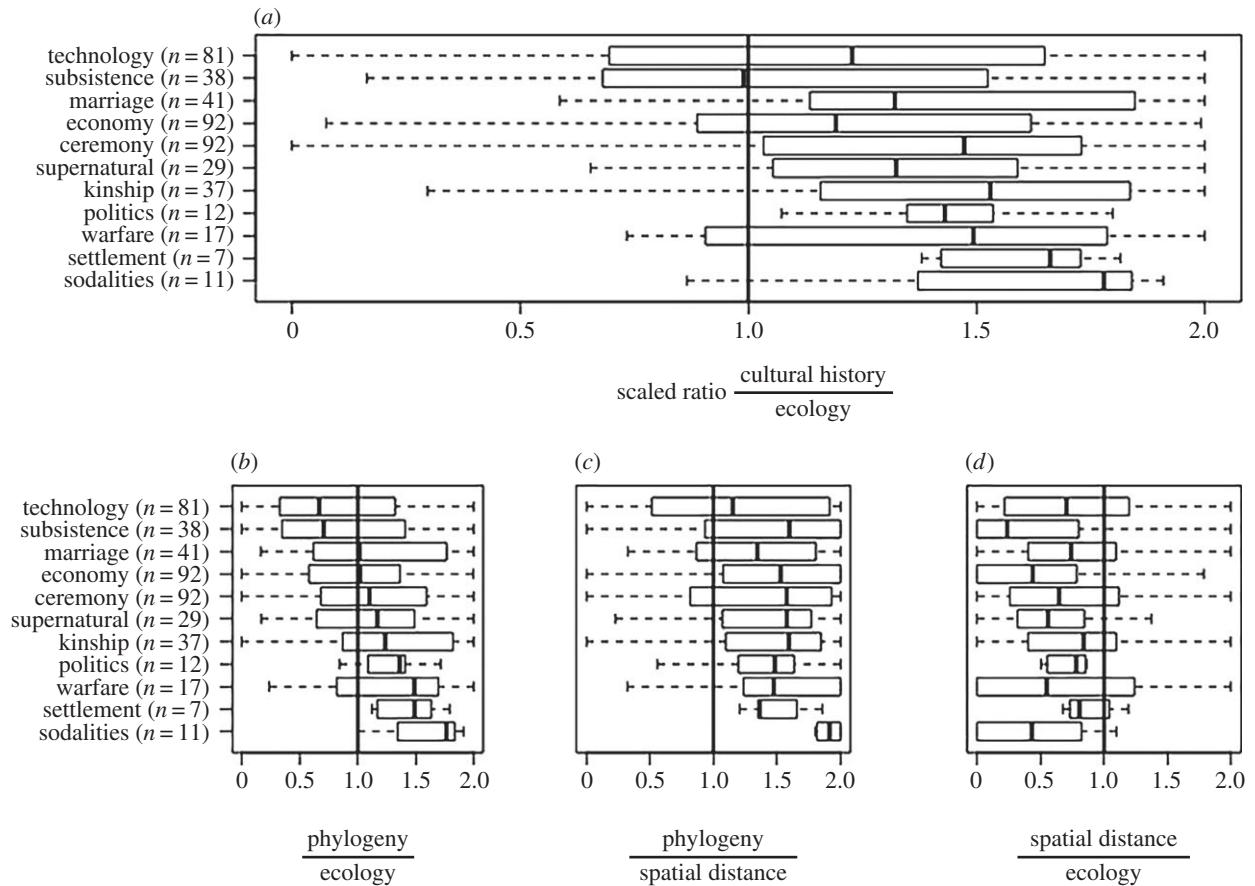rspb.royalsocietypublishing.org   Proc. R. Soc. B 282: 20150061

Figure 2. Cultural history has a larger effect than ecology in most categories of traits. Boxplots of the scaled ratios given by (a) $(\tan^{-1}C/E)/45$, (b) $(\tan^{-1}P/E)/45$, (c) $(\tan^{-1}P/S)/45$ and (d) $(\tan^{-1}S/E)/45$. The $\tan^{-1}$ scaling transforms the ratios C/E, P/E and S/E, which can range from 0 to ∞, into numbers that range between $0°$ and $90°$. This gives the slope of the line from the origin (0,0) to the coordinate (C, E), (P, E) or (S, E), respectively, which when divided by $45°$ yields a number between 0 and 2. A number greater than 1 (to the right of the vertical black line) means that the effect of the numerator is larger than that of the denominator, and vice versa.
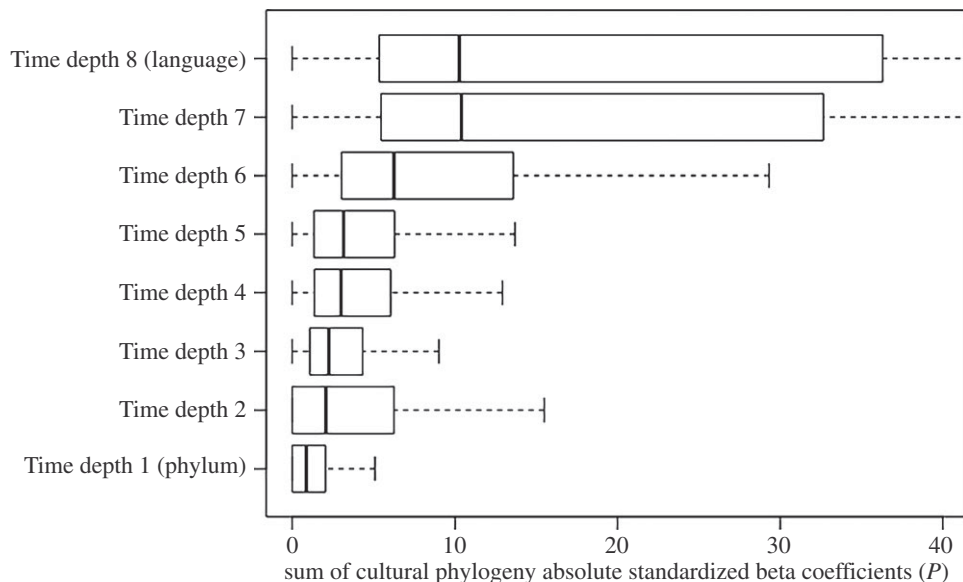

Figure 3. The effect of cultural phylogeny decreases with time, but can be detected over thousands of years. Boxplots of P using language phylogenies of different time depth. Time Depth 8 corresponds to the distribution of P when phylogeny is captured using all eight levels of the language classification, from Level 1 (phylum, the oldest level) to Level 8 (language, the most recent level). Time Depth 7 corresponds to the distribution of P when cultural history is captured using Levels 1 to 7, and so on. The x-axis is truncated for visibility.

where $\boldsymbol{\beta}^{E}$, $\boldsymbol{\beta}^{P}$ and $\boldsymbol{\beta}^{S}$ are the vectors of the standardized betas calculated from b_{E}, b_{P} and b_{S}, respectively, and n_{e}, n_{p} and n_{s} are the numbers of ecology, cultural phylogeny and spatial distance predictors, respectively, included in the best model for that trait. E, P and S are the norms of the vectors of the standardized betas for the environment, cultural phylogeny and spatial distance, and

thus represent the total effect that the environment, cultural phylogeny and spatial distance has on the probability that a trait is present or absent in a tribe. We repeated this analysis using the eight different linguistic distance matrices (from Time Depth 1 to Time Depth 8).

3. Results

Virtually all the traits are affected by both cultural history and ecology. In only three traits (less than 1%) there is no effect of cultural history (i.e. $C = 0$), and in only nine traits (2%) there is no effect of ecology (i.e. $E = 0$).

Cultural history, however, has a stronger effect on the probability of a trait being present than ecology. The distribution of C is significantly different, and has a larger median, than the distribution of E (two-sample Kolmogorov–Smirnoff test, two-sided, $D = 0.2166, p < 0.0005, n = 457$; figure 1a). Cultural history also has the largest effect on a majority of the traits. C is larger than E for 321 (70%) of the traits.

The effect of cultural history is largely driven by cultural phylogeny, not spatial distance. The distribution of P is significantly different, and has a larger median, than the distribution of S (two-sample Kolmogorov–Smirnoff test, two-sided, $D = 0.2801, p < 0.0005, n = 457$; figure 1b). The effect of cultural phylogeny is similar in magnitude to that of ecology, as the distribution of P is not significantly different from the distribution of E (two-sample Kolmogorov–Smirnoff test, two-sided, $D = 0.0744, p = 0.16, n = 457$). The effect of spatial distance is smaller than that of ecology. The distribution of S is significantly different, and has a smaller median, than the distribution of E (two-sample Kolmogorov–Smirnoff test, two-sided, $D = 0.2845, p < 0.0005, n = 457$). The effect of cultural phylogeny is largest for 219 (48%) of the traits, ecology is largest for 181 (40%) of the traits, and spatial distance is largest for 57 (12%) of the traits. In 12 traits (less than 3%) there is no effect of phylogeny (i.e. $P = 0$), and in 100 traits (22%) there is no effect of spatial distance (i.e. $S = 0$).

Cultural history has a larger effect than ecology in a majority of the traits in the categories of technology and material culture, marriage and family organization, economic organization, ceremonies and rituals, supernatural beliefs, kinship system, political organization, warfare, settlement patterns and sodalities (figure 2a). Conversely, the effect of ecology is larger than that of cultural history in a majority of the traits related to subsistence. Cultural phylogeny is a stronger predictor than ecology for a majority of the traits in all categories of traits, except for technology and material culture, and subsistence (figure 2b). It is also a stronger predictor than spatial distance for a majority of traits in all categories (figure 2c). Finally, ecology is a stronger predictor than spatial distance for a majority of traits in all categories (figure 2d). The list of traits, and the values of C, E, P and S for each trait, are provided in the electronic supplementary material.

Our analyses also show that the effects of cultural phylogeny declines over time, as the distribution of P decreases from Time Depth 8 to Time Depth 1 (figure 3). Interestingly, the largest gains in P occur at Time Depth 6 and 7, not Time Depth 8, the phylogeny that includes the language spoken by the tribes. The effect of P is minimized when using only phylum. Yet, in the model based on phylum alone (Time Depth 1; figure 3), P remains positive for the majority (52%) of behavioural traits.

4. Discussion

Cultural history, not environment, is the main determinant of behavioural variation across groups, a finding that indicates social learning to be the main mode of human adaptation. Because culture is an inheritance system, and therefore path-dependent, it sets different groups on different adaptive trajectories, even when they live in similar environments [6,21].

The results indicate that behaviours can persist over millennia within a cultural lineage. We detected a positive effect of cultural history at every phylogenetic level, including the deepest level, phylum. This is striking, since phylum divides the tribes into two groups, Na-Dene and Amerind, a split that may be as old as 15 000 years [36].

The results also suggest that groups diverge linguistically more rapidly than they do behaviourally. The largest increase in the effect of cultural phylogeny is not observed at the language level, but at the two levels below it, Levels 6 and 7 (figure 3). This would mean that a better predictor of the behavioural variation between, say, the tribes Haisla Kwakiutl, Haihais Kwakiutl, Pentlatch and Squamish, is not the specific language they speak, but rather that they speak a Wakashan or a Salishan language. An analogy would be that the best predictor of the behavioural variation in Western Europe is not whether populations speak French, Italian, German or Dutch, but whether they speak a Romance or a Germanic language.

The importance of Levels 6 and 7 imply that the behavioural repertoire of a tribe is strongly influenced by that of its ancestors that lived hundreds (if not thousands) of years ago. Levels 6 and 7 may represent shared ancestry more than 1000 years ago. For instance, the speakers of Salishan languages share a common ancestor at Level 6 and may have begun to diverge about 3000 years ago [37].

The fact that cultural phylogeny has a stronger effect than spatial distance on the presence of behavioural traits indicates that learning from group members is a more important process than learning from members of other groups. This may reflect the effects of conformism [11], norm enforcement [38,39], parochialism [40–42], group coordination [43], barriers to trade across ethnolinguistic groups [1,24] or the need for close proximity to models [44].

The results indicate that the richness of our behavioural repertoire may be due in large part to our capacity for culture, and not exclusively to non-cultural mechanisms. These non-cultural mechanisms, such as causal reasoning, inventiveness, trial-and-error learning, rational choice decision-making, reaction norms or the cognitive modules that shape behaviour in response to ecological input, have been emphasized by the cognitive niche hypothesis [16], human behavioural ecology models [12,17–20] and the evoked culture theory [7,14]. Instead, we found social learning operating over multiple generations to be the main mode by which humans acquire their behaviour. The theories that exclude these mechanisms may thus be useful to study other species but are ill-equipped to deal with humans [45].

A next step is to explain what aspects of the evolved mind make our species uniquely capable of acquiring and transmitting culture. On the one hand, human culture may be a mere by-product of domain-general intelligence. The increase in brain size in our lineage may have resulted in an increase in domain-general intelligence that allowed humans to expand their behavioural repertoire by

incorporating new sources of information, such as the behaviour of conspecifics. On the other hand, human culture may be the product of cognitive machinery that has been designed by natural selection specifically to acquire information from conspecifics [46]. For instance, there is evidence that humans have domain-specific cognitive adaptations that harness socially transmitted information in order to learn which plants are edible [47], and which animals are dangerous [48].

Our results do not imply that non-cultural mechanisms are unimportant. First, the effect of ecology is not trivial and is especially important in traits related to subsistence. Moreover, our analysis examines behavioural variation between groups. The respective effect of ecology and cultural transmission on behavioural variation between groups may be different from their effect within groups. Second, as described above, human psychology may have evolved in response to our heavy reliance on social learning [46–48]. Third, causal reasoning and inventiveness will increase rates of innovation, and thus influence how fast cultural adaptations can emerge. Finally, culture allows humans to modify their environments, for instance by making fire, domesticating plant species or building shelters, a process

called niche construction [49]. Humans also modify their social environments through culturally transmitted institutions, such as property rights systems, marriage rules and the policing of norm violators. Thus, single-generation adaptive mechanisms in humans may have evolved primarily to respond to these culturally constructed environments. The interaction between these mechanisms and culture may explain why humans were able to expand rapidly into virtually every terrestrial habitat on the planet.

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