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Problems modelling behavioural variation across Western North American Indian societies

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Mathew & Perreault [1] analyse cross-cultural data from the Western North American Indian (WNAI) dataset [2] in order to compare 'the relative effect of environment and cultural history' on behavioural variation across 172 societies. This endeavour is inspired by many other evolutionary studies of human cultural variation [3–7]. Mathew and Perreault conclude that 'social learning operating over multiple generations [is] the main mode by which humans acquire their behaviour' (p. 5). Our own investigation of cultural macroevolution in the WNAI [8] motivated us to attempt to reconstruct their analyses. we found their paper to be undermined by questionable analytical choices, and computational and data-handling problems. We draw this conclusion having used the information in the Methods and electronic supplementary material S1, S3, S4 and S6 in [1] to recreate those parts of their study that we were able to. In this commentary, we present the results of our examination and detail the serious methodological flaws that lead us to conclude that a complete re-analysis is required by Mathew and Perreault. We also comment briefly on their conceptual schema, which, in trying to find 'the main mode of human adaptation' [1], appears to set cultural transmission (i.e. social learning) in opposition to environmental adaptation.

Mathew and Perreault use logistic regression to model 457 present/absent behavioural traits as a function of three dimensions—E (local ecological conditions), P (phylogenetic or linguistic distance to other societies) and S (spatial or geographical distance to other societies). To judge the relative importance of the E, P and S classes of predictors, Mathew and Perreault compare sums of absolute values of regression coefficients across classes, for the best model of each behavioural trait. The 'summed absolute values' metric is used for various purposes in model and feature selection [9,10]. The metric is problematic here, however, because it compounds statistical signal with different sizes of the E, P and S classes. To demonstrate, consider a null case in which none of the predictors in E, P or S are related to a trait and the regression coefficients resemble stochastic noise. The analyst must understand how a statistical metric would behave in such a case and choose an inference procedure that reliably distinguishes null from non-null cases. For concreteness, assume that the coefficients share a common Gaussian distribution with mean zero and variance σ^2. The absolute value of a coefficient β then has expectation $(2\sigma^2/\pi)^{1/2}$, and for a class containing M predictors the summed absolute values have expectation $E[\sum_{i=1}^{M} |\beta_i|] = M(2\sigma^2/\pi)^{1/2}$. The null expectation therefore scales linearly with class size M, and larger classes of predictors will appear to have greater relative importance based on representation alone. Although model selection criteria such as AIC (discussed below) include a penalty for the number of predictors in a model, this does not mitigate the confounding effects of class size [11].

To see how summed absolute values depend on the number of predictors contributing to the sum, consider fig. 3 of [1], which appears to show a time-depth effect of language. The numbers of predictors in phylogenetic classes, from the Level 8 class down to the Level 3 class, follow a descending sequence: $M = 8, 8, 6, 4, 4, 3$ (see electronic supplementary material S7 in [1]). This sequence is mirrored by the stair-step feature of the overall effect of phylogeny and is
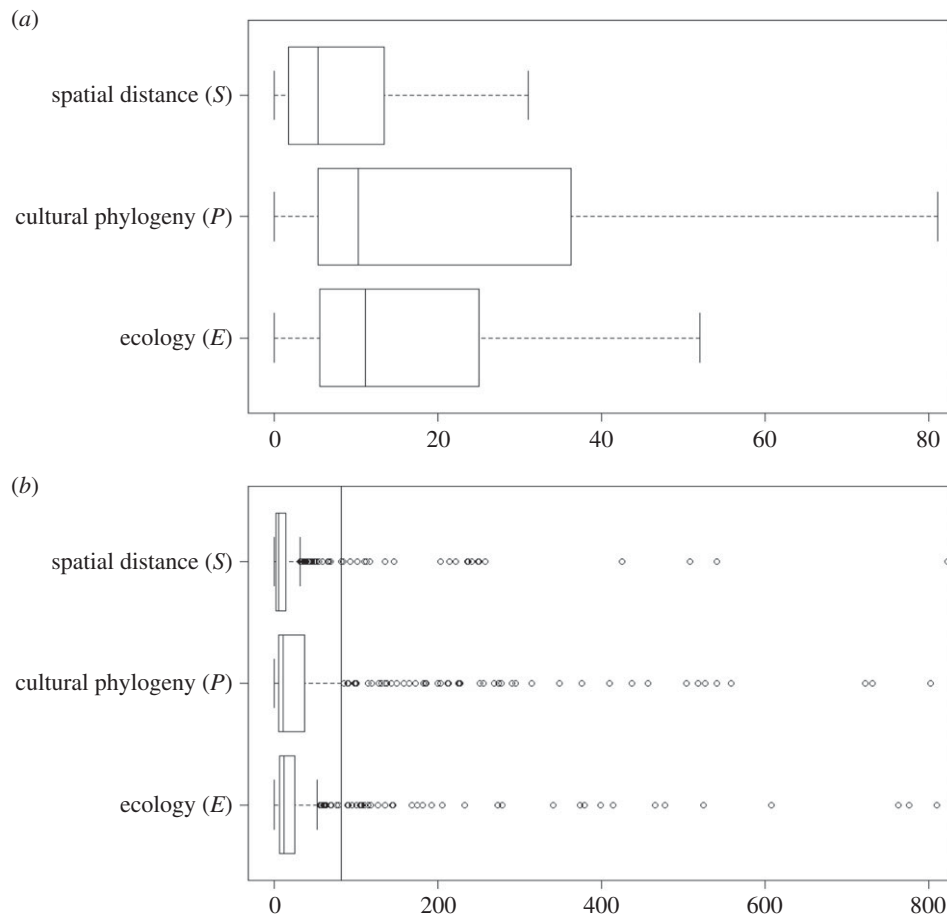
2

Figure 1. Boxplots of summed absolute standardized β coefficients for S, P and E: (a) reproduction of fig. 1b in [1], without outliers and truncated at a summed value of 80 (omits 35 S, 83 P and 54 E values > 80); (b) modified figure of the same data, including outliers and truncated at a summed value of 800 (omits 13 S, 31 P and 18 E values > 800).

wholly consistent with null expectations. Thus, what Mathew and Perreault interpret as greater relative importance for predictors incorporating deeper history may reflect only the fact that the deeper-level classes contain more predictors—interpretation of the figure is precluded by confounding effects of class size. The ratios of importance values shown in their fig. 2 are also consistent with null expectations. For example, with $M = 6$, 8 or 3 (for classes E, P or S, respectively), the null expectation of the relative importance of cultural history over ecology, $(S + P)/E$, is approximately 11/6, yielding 1.4 after $\tan^{-1}$ scaling (see their fig. 2 caption). The value 1.4 (not 1.0) is thus a more appropriate null reference for fig. 2a in [1]. Boxplot medians in fig. 2a stay relatively close to this value. As 11 of the 17 (65%) predictors are assigned to cultural history, it is not surprising that the overall effect for this combined class is larger than that for ecology in 70% of the behavioural traits. In short, the relative strengths of E, P and S cannot be discerned as Mathew and Perreault intend without a correction for the number of predictors in each class.

The overall effects reported by Mathew and Perreault are also troubled by numerical instability. For instance, the outcome 'salt added to food' (r_tech_162) has absolute sums of 4.29×10^{15}, 3.20×10^{15} and 1.05×10^{16} for E, P and S, respectively (see electronic supplementary material S6 in [1]). Models for at least 29 outcomes have extreme effect sizes, even after dividing by class size M. Logistic regression coefficients predict changes in the log-odds of a binary outcome per unit changes in the independent variables. For reasons described by Gelman et al. [12], large-magnitude

coefficient estimates call for special scrutiny and may indicate underlying problems such as non-convergence of model-fitting algorithms, variable separation or multicollinearity. In fact, in reproducing their results, we found that 24 of 457 models failed to converge; 12 of these were among the models with extreme effect sizes. Rather than addressing such problems directly, Mathew and Perreault take measures such as truncating axes (figure 1 above, and figs 1 and 3 in [1]) and rescaling coefficients by a $\tan^{-1}$ transformation (fig. 2 in [1]), the latter apparently to control the infinite relative importance values that result from division by zero.

During our reconstruction of the analyses, we also uncovered a critical flaw in Mathew and Perreault's use of principal component analyses (PCA) to compute P and S dimensions. To determine the predictors in P and S, Mathew and Perreault pass a matrix of pairwise distances (spatial or linguistic) to the *prcomp* function in the R language [13]. This function is designed to operate exclusively on datasets consisting of sampling units (here, cultures) in rows, and measured attributes (features) of these units in columns. In their columns, Mathew and Perreault use relational data—pairwise distances—where *prcomp* expects cultural attributes. In figure 2, we demonstrate the consequences of this for the spatial components. To visualize analogous consequences for the phylogenetic components is a more challenging problem we have not solved. Given the functionality of *prcomp*, however, we expect similar distortions because the components are calculated using relational distances along a language tree, not primary attributes of the individual cultures.
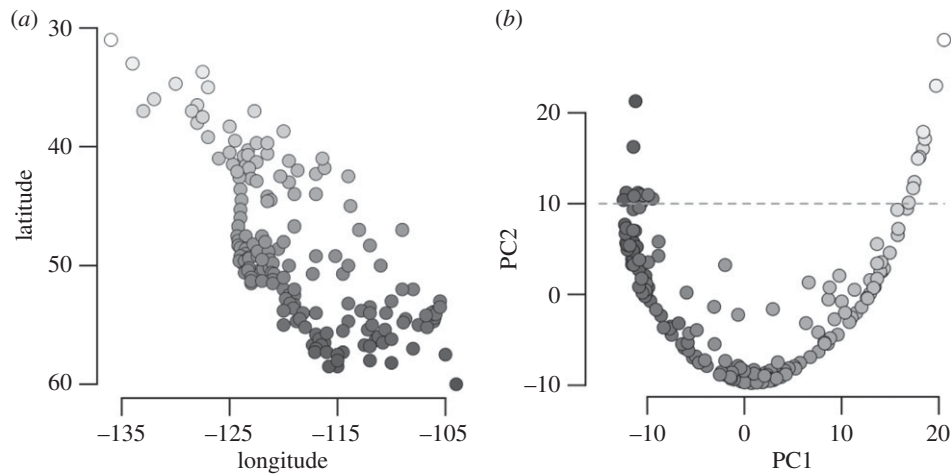
Figure 2. Spatial warping produced by PCA on a pairwise distance matrix: (*a*) cultures plotted by Lat/Lon coordinates, with points shaded by a latitudinal gradient; (*b*) cultures plotted by spatial PC scores on dimensions one and two (data obtained from electronic supplementary material S1 in [1]), with shading scheme carried over from panel (*a*). PCA on the pairwise distance matrix introduces artificial nonlinear relationships between cultures and compresses spatially distinct cultures along a parabolic curve. The dashed horizontal line at PC2 = 10 demonstrates that cultures well separated by latitude may share the same value on PC2. Shading by a longitudinal gradient produces similar graphs. Spatial relationships adequately described by latitude and longitude together are obscured in the PC space.

One alternative to PCA is principal coordinates analysis (PCoA), a related method specifically for pairwise distance matrices [14]. The first two dimensions of a PCoA applied to spatial distances closely recreate spatial configurations at moderate scales (see example 5.2 in [15]). For discrete, low-variation distances like those produced by the language tree, PCoA may not be as suitable. A second alternative to PCA makes direct use of phylogenetic and spatial distances in a parametrized variance–covariance matrix [16]. Whatever the relationships are between cultural traits, phylogenetic and spatial distances, they may be disrupted by inappropriate use of PCA.

Mathew and Perreault use the *glmulti* package in R to screen all 131 071 possible models for each trait and then analyse the coefficients of just the single best model—the model with the lowest AIC value (AIC_{min}). Model comparison is a powerful tool for evaluating alternative models given the data [12,17]. However, given so many predictors, the best model is often one of a large set of models with very similar AIC values (e.g. $\Delta_i < 4$, where Δ_i is defined as $AIC_i - AIC_{min}$), and our analysis of their data suggests this is true for most traits. As detailed by Burnham & Anderson [11], model averaging combines information from a set of top models, and thus incorporates more sample information and produces more robust inferences (e.g. about the relative effects of *E*, *P* and *S*). Moreover, the coefficients associated with each predictor can be interpreted in the context of other predictors, even if the single best model leaves out a particular component. Alternatively, rather than screening all possible models, Mathew and Perreault could compare *a priori* sets of models with different combinations of components (e.g. *EPS*, *EP*, *ES*, *PS*, *E*, *P* and *S*) [18].

The accumulation and transmission of cultural knowledge are hallmarks of the human species [19], and cross-cultural variation demonstrates strong regional and linguistic patterning [20]. Likewise, both abiotic and biotic environments clearly shape and constrain human cultural behaviour (see [21] for a review and [22] for a detailed study of resource-defence polygyny in the WNAI). We thus question the central framing of Mathew and Perreault's study—as a test for whether human behavioural variation 'is due to variation in the ecological environment or to differences in cultural traditions' (see abstract of [1]). Their apparent posing of non-cultural mechanisms against cultural mechanisms is problematic in two main ways. First, it fails to acknowledge that social learning is itself an adaptation to the patterning of environmental change over time [23]. Second, we do not believe that anyone has seriously proposed that the decisions humans make regarding behavioural strategies emerge de novo with each generation (Mathew and Perreault's 'single-generation adaptive response' caricature) [24–26], nor have they ever done so [21]. Mathew and Perreault undoubtedly recognize the complexities here, and in places acknowledge the complementarity of perspectives. Nevertheless, we caution that framing a paper as a debate detracts from the more interesting challenge, which is to determine the relative influences of different transmission mechanisms, recognizing that they operate in addition to—not as alternatives to—adaptation [3,4,19,25]. Furthermore, careful modelling in this area indicates that given the complexity of interacting factors, we are still far from being able to use patterns in space and time to pinpoint the mechanisms responsible for cultural diversity [27].

For over a century, anthropologists have endeavoured to understand the origins and maintenance of cultural variation across human societies [28], and an evolutionary ecological perspective such as that of Mathew and Perreault has much to contribute [3–8]. Although such investigations have proved to be methodologically challenging, the field has prospered as many alternative quantitative approaches have been developed, employed and compared. Unfortunately, Mathew and Perreault's analyses are hampered by numerous problems that make it impossible to draw any reliable conclusions from their results. In conclusion, we believe that the statistical and computing mistakes in Mathew and Perreault are serious enough to merit a complete re-analysis of the data, particularly given the importance of understanding the multiple mechanisms responsible for the origins and maintenance of cultural variation across human societies.

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Invited reply

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Cultural history, not ecological environment, is the main determinant of human behaviour

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Towner *et al.* [1] question the methods and the theoretical framework of our study of behavioural variation among Native American tribes of Western North America [2]. Here we show that their concerns are unfounded and that our results are robust. We also clarify the theoretical issues that motivated our paper, and explain why it is critical to disentangle the role of ecology and cultural inheritance in a cultural species like humans.

Towner *et al.* contend that the higher summed absolute value of the cultural–historical betas (i.e. C) relative to that of ecology (i.e. E) is due to the fact that cultural history has 10 potential predictors and ecology has seven. Their argument is based on the fact that the expectation of the absolute beta of a predictor representing stochastic noise is not zero, but $(2\sigma^2/\pi)^{1/2}$ (assuming the coefficients are drawn from a Gaussian distribution with mean zero and standard deviation σ). This is because the probability density on the negative side of the distribution of beta is shifted to the positive side in the distribution of the absolute beta. Thus, any predictor in a model will contribute to C or E, even when they represent stochastic noise. Towner *et al.* suggest that the correct measure of the effect size of cultural history and ecology is $C - M_C(2\sigma^2/\pi)^{1/2}$ and $E - M_E(2\sigma^2/\pi)^{1/2}$, where M_C and M_E are the number of cultural historical and ecological predictors, respectively.

We show here that this correction is not necessary, and neither does it change th results. The model selection approach shields our results from the effect of predictor class size. Predictors that represent stochastic noise will have betas with large standard error relative to their effect size. Such predictors are unlikely to be included in the best model, as the Akaike information criterion (AIC) penalizes models for the number of predictors they contain. As a result, the absolute value of a β coefficient in the best model is a good measure of the true absolute magnitude of the effect of that predictor, even if it does not incorporate explicitly the standard error of the β estimate.

However, explicitly incorporating the standard error of the β estimates, as Towner *et al.* suggest, is a valid alternative to the approach we used. But Towner *et al.*'s correction is incomplete, because it is only applicable to the worst-case scenario where the predictors represent stochastic noise. Just as the expectation of the absolute beta of a predictor representing stochastic noise is shifted from zero to $(2\sigma^2/\pi)^{1/2}$, the expectation of the absolute effect of a predictor with mean β and standard deviation σ is

$$E(|\beta|) = \beta - 2\int_{-\infty}^{0} x\,\frac{1}{\sigma\sqrt{2\pi}}e^{((x-\beta)^2/2\sigma^2)}.$$

Thus, the absolute effect of a predictor, β', is the difference between $E(|\beta|)$ and the null expectation

$$\beta' = \beta - 2\int_{-\infty}^{0} x\,\frac{1}{\sigma\sqrt{2\pi}}e^{-((x-\beta)^2/2\sigma^2)} - \left(\frac{2\sigma^2}{\pi}\right)^{1/2}. \tag{1.1}$$

The extent to which β' differs from $|\beta|$ depends on the extent to which the density of the distribution of the β coefficient encompasses both negative and

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positive values. When the magnitude of an effect size is large relative to the standard error, $\beta' - |\beta|$ will be small, and vice versa. Because the best model is unlikely to contain predictors with small effect size relative to standard error, it is not surprising that when we reanalyse the data using Towner et al.'s approach, we get the same results as before (electronic supplementary material, figures S1–S3).

Towner et al. claim that our results are driven by the fact that 29 out of 457 traits have extremely large betas. This is not the case. Our results are unchanged by the removal of these 29 traits (electronic supplementary material, figures S4 and S5).

Towner et al. are confused about our use of the arc tan transformation. The arc tan transformation is a natural way to calculate the ratio between effect sizes when effect sizes can be zero. Consider a trait with two summed absolute values, C and E. The arc tan transformation represents the relative magnitude of C and E as the slope, ranging from $0°$ to $90°$, of the line that goes from the origin to the coordinates of a trait (electronic supplementary material, figure S6).

Towner et al. argue that analysing the linguistic matrices with the prcomp function is problematic, because the prcomp function cannot operate on pairwise datasets, but only on datasets consisting of sampling units in rows and measured attributes in columns. It is obvious from the dimensions of the linguistic matrices (172×116, 172×85, etc.) that the matrices are not pairwise. More importantly, the rows of the linguistic matrices are our sampling units (i.e. tribes) and the entries in the columns are attributes (i.e. the language group to which a tribe belongs). Similarly, the rows of the spatial distance matrix represent the sampling units (i.e. tribes), and the entries in the columns are attributes (i.e. the distance from potential sources of diffusion).

Towner et al. suggest that we should assess the importance of ecology and cultural history by finding which of a set of a priori models performs the best according to some information criterion. For example, cultural history will be considered an important determinant of a trait if the AIC of the model that includes both cultural historical predictors and ecological predictors is lower than the AIC score of a model including only ecological predictors. Given our research question, this approach is inadequate, as it provides no information about the relative effect sizes of ecology and cultural history. Our analysis not only shows that the best models include both ecology and culture predictors for almost all of the traits, but it also specifies the relative magnitude of their effects.

Towner et al. also misunderstand the theoretical issues that motivated our paper. They argue that our comparison of the effect of ecological environment and cultural history is flawed (i) because it fails to acknowledge that social learning is itself a mode of adaptation to the environment, (ii) because nobody has ever seriously proposed that behavioural strategies emerge de novo with each generation, and (iii) because the interactions between the mechanisms underlying behaviour are too complex to be studied.

First, we did acknowledge that social learning leads to behaviours that are adapted to local environments. This is what we meant when we wrote 'social learning can also lead to behaviours that are adapted to local environments'. Therefore, the effect of ecology may not only be due to single-generation adaptive mechanisms, such as trial-and-error learning and reaction norms, but also due to the effect of cultural adaptations to local ecology. In contrast, the effect of cultural history can only be attributed to social learning, because only social learning (genetic evolution aside) operates over multiple generations. Thus, our estimate of the effect size of cultural history is a conservative measure of the effect of social learning as it excludes rapid cultural adaptations to environments.

Second, behavioural strategies do emerge de novo with each generation among all animal species, including humans. No one doubts that animals respond to their environments through non-social adaptive responses, such as evolved heuristics, trial-and-error learning, reasoning and developmental plasticity. These non-social adaptive mechanisms will lead to de novo emergence of behaviour each generation as individuals independently converge on the same behaviour. Given the importance of these mechanisms in the world of non-human animals, it is important to ask what role they play in humans. Thus, it is not surprising that a number of researchers have stressed the importance of these mechanisms at the expense of cultural mechanisms [3,4].

Third, Towner et al. would like us to give up on comparing the effect of cultural and non-cultural mechanisms, because their interactions are too complex. Their logic is puzzling. Anthropologists have long been disentangling the effect of cultural history from that of the environment. As early as the late nineteenth century, social scientists recognized that societies can be similar not because they have converged on the same behavioural strategies independently, but because they share a cultural ancestor. Recently, anthropologists, including some of the co-authors of the comment, have advocated for the use of cultural phylogenetic methods in order to control for shared ancestry [5]. The premise of cultural phylogenetic methods is that the effect of shared ancestry can be separated from that of the other mechanisms that shape human behaviour. If Towner et al.'s argument is valid, then these efforts at controlling for shared ancestry are misguided.

The difference between our approach and cultural phylogenetic methods is that our approach puts shared cultural ancestry on equal footing with the other predictors. This allows us to quantify its effect size on the same scale as the other classes of predictors. In contrast, cultural phylogenetic methods treat shared ancestry as a factor that needs to be muted in order to reveal what is scientifically interesting. Whereas these methods were developed to test adaptive hypotheses about human behaviour, they may be silencing the main mechanism that gives rise to human adaptation, cultural evolution over multiple generations.

Towner et al.'s view is also at odds with the study of trait heritability in biology. Like culture, genes form an inheritance system. Researchers routinely partition the effect of genes and environment on all sorts of traits, including behavioural traits. In doing so, they compare the effect of shared genetic ancestry with that of other sources of phenotypic variation, such as developmental plasticity, reaction norms and learning. It would make no sense for biologists to refrain from efforts to disentangle the effect of genes and environments on the basis that they both interact in complex ways to give rise to phenotypes.

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