Title

Tradeoffs and cultural diversity

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Abstract

Culture is humanity's prime adaptation. Which cultural traits contribute to adaptive value, and how they do so, is however, unclear and debated. Here, we apply an approach from systems biology, known as Pareto task inference (ParTI), to bring a fresh perspective to these questions. ParTI considers biological systems that need to perform multiple tasks. No system can be optimal at all tasks at once, leading to a fundamental tradeoff. Such tradeoffs constrain evolution, because adaptive change for one task may be prevented because it compromises other tasks. These constraints result in specific patterns in multivariate trait data: data falls inside polygons in trait space, whose vertices are trait complexes that are adaptive for each of the tasks. ParTI detects these polygons and their vertices, in order to infer the number of adaptive tasks and their nature. Here, we applied ParTI to two datasets of human cultural traits, on Austronesian cultures and modern hunter-gatherers, adjusting for phylogeny and spatial diffusion effects. We find that these independent datasets show the hallmarks of a tradeoff between the same three tasks. We identify the tasks as resource defense, resource competition, and mobility/exchange. Specific combinations of cultural traits are adaptive for each of these tasks. We thus find evidence that at the macro, between-society level, part of the diversity of human cultural traits is constrained by tradeoffs between key tasks, explaining why certain combinations of traits recur, whereas other combinations seem to be missing.

Introduction

Evolving systems often need to perform multiple tasks, and performance in each task contributes to fitness. This leads to a fundamental tradeoff, because no phenotype can be optimal at all tasks at once. Such tradeoffs have long been recognized to be a major constraint on evolution[1,2]. For example, a bird's beak may provide fitness from the tasks of eating seeds and eating pollen. Seeds require a beak shaped like a plier, whereas pollen requires a beak shaped like pincers. No single beak phenotype can be optimal at both tasks. Other examples include tradeoffs between reproduction and survival[3] and between clutch size and offspring size[4]. Tradeoffs are important also at the level of cells[5], such as the tradeoff between bacterial growth and survival[6], and at the level of proteins[7], and organs[8].

In most studies on tradeoffs, researchers propose the tasks a-priori. However, in some cases the tasks cannot be easily determined in advance. To address this, a recent theorem allows inferring tradeoffs and identifying tasks directly from data on multiple traits. This approach, called Pareto task inference (ParTI), links the geometrical structure of high-dimensional phenotypic data to its evolutionary tradeoffs[6]. ParTI was used to define evolutionary tasks and tradeoffs in gene expression in cells[6,9–11], development[12], animal morphology[6,13], behavior[6], and life-history strategies[14] (Supplementary Information 1).

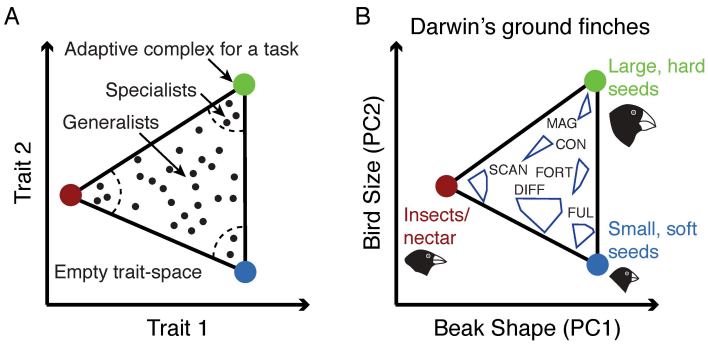

Figure 1. Triangular structure of biological data shaped by three tasks with tradeoffs. A) According to multi-task evolutionary theory, when three tasks with tradeoffs are present we expect the observed trait combinations to fall within a triangle. Each vertex of the triangle corresponds to an adaptive complex for a single task, and the data points closest to that vertex are specialists for that task. Points at the center of the triangle are generalists. B) Darwin's finches, measured for five morphological traits fall on a triangle whose axes are the two first principal components of the five traits[6]. The three tasks of the adaptive complexes can be inferred from the specialization of the species closest to each vertex: eating large seeds, small seeds and insects/nectar. Other species are generalists that combine these tasks.

ParTI considers the case where fitness is determined by performance at several tasks at once. ParTI theory shows that the best tradeoff trait combinations fall inside low-

dimensional polygonal shapes in trait space (Figure 1AB). These shapes have vertices and flat sides, such as lines, triangles, tetrahedra and so on[6]. Each vertex is an adaptive complex of traits that is optimal for one of the tasks. For two tasks, the data should fall in a line segment between the two adaptive complexes; for three tasks, it should fall in a triangle with the three adaptive complexes at the vertices and so on. For example, as shown in Figure 1B, Darwin's finches' beaks fall on a triangle with three vertices that correspond to eating small seeds, large seeds and pollen. Specialists at each task lie near a vertex, and generalists lie in the center of the triangle. The intuitive reason for the triangle is that any point outside of the triangle has a point inside the triangle that is closer to all three vertices, and hence has better performance at all tasks and hence higher fitness.

To determine the number and nature of the tasks, ParTI algorithms determine the best-fit polygon that describes the data and its vertices. The number of tasks is equal to the number of vertices. The nature of the tasks need not be assumed in advance; instead, the tasks can be inferred from the properties of the data points that are closest to each vertex[9] (Figure 1B). ParTI applies to any type of process that increases adaptive value, not only genetic evolution.

Here, we apply the ParTI approach to study tradeoffs in human cultural datasets. Cultures are remarkably diverse, and this diversity is key to explaining humanity's success in inhabiting most of the earth's terrestrial environments[15–17]. However, the adaptive origins of the distribution of cultural traits remains unclear and debated[18–20]. While many studies examined adaptive cultural behavior at the level of the individual, only few tested adaptive hypotheses about behavioral or cultural diversity at the between-societies, macro-level[21,22]. So far, no study has directly inferred the impact of tradeoffs on macro-level cultural adaptation, without assuming what the tasks are in advance. Given the crucial role of tradeoffs in biological evolution, it is important to examine whether tradeoffs can be detected also in cultural traits and if so, between what tasks.

To test the role of tradeoffs in shaping cultural diversity, we apply ParTI to cultural traits in human societies using multivariate cross-cultural datasets. We hypothesize that the adaptive advantage of cultural traits is due to their contribution to several tasks, whose number and nature is unknown a-priori. ParTI predicts that the adaptive part of the variation between cultures should therefore lie in a polygon in cultural trait space. The number of vertices of the polygon corresponds to the number of tasks, and the features found in the cultures nearest each vertex should provide clues to the nature of the tasks, while controlling for phylogeny and spatial diffusion effects.

Methods

Cross-cultural datasets. The *Pulotu*[23] dataset on traits of 113 Austronesian cultures, linked to a language-based family tree, was downloaded from https://pulotu.econ.mpg.de/. We used traits that are cultural (i.e. not physical) and belong to the traditional time focus as defined by Watts et al.[23] (see Supplementary Information 2 for information on data preparation).

Binford's Hunter-Gatherer (BHG)[24] which includes cultural traits for 339 modern hunter-gatherer cultures, was downloaded from http://ajohnson.sites.truman.edu/data-and-program/ (see Supplementary Information 3 for information on data preparation). The two datasets differ both in the mode of subsistence of societies that are included (*Pulotu* includes mostly agricultural societies) and in the cultural traits measured, which are largely non-overlapping between the datasets. In Supplementary Tables 1,2 we list the traits used for our analysis (codebooks for traits are available in the links above). Importantly, we verified that the results are not confounded by the structure of the dataset. That is, the empty regions in the trait-space of both datasets consist of (a-priori) feasible trait combinations (see Supplementary Information 5 for discussion).

Language tree phylogenies. To generate a phylogenetic null model for principal component analysis and for triangle statistical significance, we used a tree with informative branch lengths for 93 Austronesian cultures from the *Pulotu* dataset (see Watts et al.[25]), `tree1`. For phylogenetic adjustment of enrichment calculations, which does not require informative branch lengths, we constructed a larger tree, `tree2`, by adding the other Austronesian cultures according to their language families (`tree2`, provided in Supplementary Information 8). Similarly, we constructed a phylogenetic tree for the cultures in *Binford's Hunter-Gatherer* according to language families (`tree3`, provided in Supplementary Information 9).

Number of significant principal components. To test the effective dimensionality of *Pulotu*, we determined the number of principal components that cannot be explained by a phylogenetic null model in which cultural traits are acquired and lost at random based on `tree1` (see Supplementary Information 4 for details).

Polytope inference and statistical significance. To infer the vertices of the polytopes (polytopes are the generalization of polygons and polyhedra to higher dimensions) we applied Principal Convex Hull Analysis (PCHA)[9,26] as implemented in the python package *py_pcha*. We tested statistical significance of triangles by using the t-ratio test as specified by Shoval et al.[6]. The t-ratio is the ratio between the areas of the convex hull of the data and the area of the minimal enclosing triangle. The close the t-ratio to one, the more the data fills out

the triangle. A p-value for the triangle was computed by the probability that the t-ratio of shuffled data is smaller or equal to the t-ratio of the real data based on 10,000 data shuffling. (see Supplementary Information 5 for details).

Feature enrichment calculation. We tested for enrichment of features by performing regression, where the response variable is the feature and the predictor variable is the Euclidean distance from vertex in the space of the first two PCs. To adjust for spatial and phylogenetic effects, we added to each regression, and for each feature, covariates for the average feature value among the 10 nearest phylogenetic neighbors (tree2 and tree3) and 10 nearest spatial neighbors (see Supplementary Information 6 for details), similar to the adjustment performed by Botero et al.[27]. For binary variables, we performed logistic regression, and for other variables, we performed linear regression.

Results

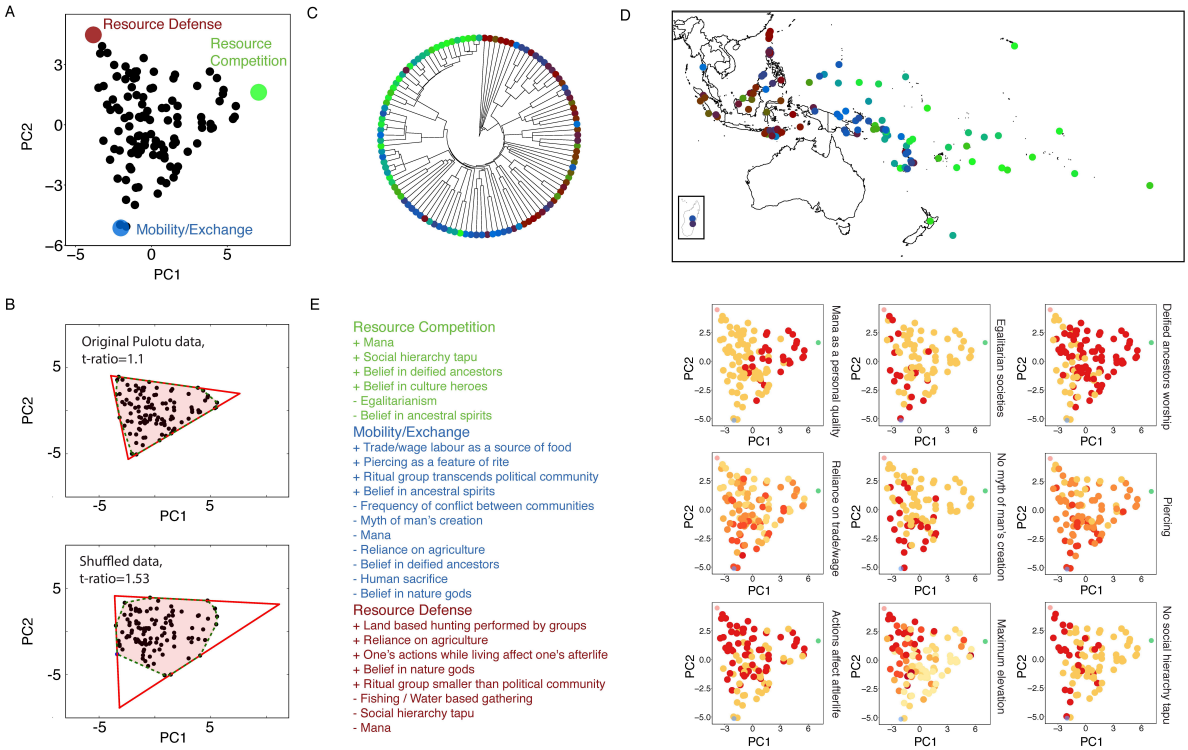

Figure 2. ParTI analysis of *Pulotu* dataset suggests three adaptive complexes. (A) *Pulotu* cultural traits are well described by a triangle ($p<10^{-3}$) in the plain of the first two principal components. The three vertices of the triangle correspond to adaptive trait complexes for the putative tasks of mobility/exchange, resource defense and resource competition. (B) To test for statistical significance, we used the t-ratio test[28] . The t-ratio is the ratio between the areas of the convex hull (pink) and the area of the minimal enclosing triangle. A t-ratio close to one means the data fills the triangle. (C) A consensus language tree for Austronesian languages. Cultures are color coded according to their relative distance from each vertex of the triangle. (D) A geographical map, with color coding as in C. (E) To infer tasks for each vertex, we seek traits that appear at higher frequency in the data points closest to the vertex. Such strongly enriched traits are listed. Sign (+/-) indicates positive or negative

enrichment. Nine of the enriched traits are visualized on the data points, with red (yellow) corresponding to a high (low) level of the trait – for example, lack of a myth of mans' creation is found predominantly in cultures near the mobility/exchange vertex, whereas deified ancestor worship is frequent in cultures closest to the resource competition vertex.

ParTI analysis of Pulotu dataset

Using ParTI analysis, we find that the distribution of traits for the *Pulotu* cultures are well described by a triangle ($p<10^{-3}$) (Figure 2A, Supplementary Information 5). We plot this triangle in the plane of the first two principal components, which explain 20% of the variance and are significant compared to a phylogenetic null model (methods). The triangle is populated by cultures almost uniformly. Many a-priori possible combinations of traits do not seem to occur, resulting in the empty trait-space around the triangle. Shuffled data does not fill in a triangle (Fig 2B).

According to Pareto theory, this triangle indicates three tasks that have tradeoffs between them. The three vertices of the triangle are adaptive complexes of traits for these three tasks (see Table S1 for the adaptive complexes). Below, we infer the three putative tasks. For clarity, we now label the three vertices by these tasks – Resource Competition, Mobility/Exchange and Resource Defense.

In order to study the relation between the traits and language phylogeny, we displayed the cultures on a language tree. We color-coded each culture according to its distances from the vertices of the triangle (Fig 2C). For example, cultures colored red are closest to the Resource Defense vertex on the triangle. We note an early-late phylogenetic gradient, from Resource Defense to Mobility/Exchange to Resource Competition. Similarly, we displayed the cultures on a geographical map (Fig 2D), showing an east-west geographical gradient from Resource Defense to Mobility/Exchange to Resource Competition. There are notable exceptions in which cultures that are close geographically and phylogenetically are not close on the triangle (Figure 2CD), suggesting that geographical proximity and phylogenetic inertia are not the only forces at play. Below, we adjusted for phylogenetic and geographic gradients in our analysis.

Characterization of adaptive complexes for *Pulotu*

To characterize the underlying tasks, we asked which cultural traits characterize the cultures closest to each vertex. For this purpose, we used regression for each trait on its distance on the triangle from each vertex, adjusted for spatial and phylogenetic effects (Methods). Each of the three adaptive complexes shows distinct cultural traits (Figure 2E).

The cultures closest to the Resource Competition vertex are the stratified Polynesian cultures[29]. Closeness to this vertex is strongly associated with *mana* (supernatural power), especially when linked with descent and social status, and with the worship of deified ancestors. These traits are related to colonization and conquest - founders of colonies become revered ancestors and their descendants enjoy high status ("founder-focused ideology")[30,31]. Other traits found near this vertex include low egalitarianism and the existence of a social hierarchy *tapu*.

The Mobility/Exchange vertex is associated with cultures that live in areas of low resource density. The cultures closest to this vertex include the sea-nomad cultures of *Sama Dilaut* and *Moken* and the sea dwelling people of *Manus*. The Polynesian and Micronesian cultures that lie on low atolls are also close to this vertex (Supplementary Information 7). The Mobility/Exchange vertex is enriched with infrequent conflict between communities, high reliance on trade and wage labor rather than on agriculture, and large ritual social groups that transcend political communities. It is enriched with piercing as a feature of rite, as well as with belief in ancestral spirits (which have a smaller sphere of influence than do deified ancestors). Otherwise, this vertex is characterized by its lacks in religious complexity – lack of *mana*, lack of human sacrifice, lack of a myth of man's creation, and lack of belief in deified ancestors and in nature gods.

The third vertex, Resource Defense, is enriched with highlander cultures that rely on agriculture and land-based hunting as opposed to fishing and water-based gathering, as well as with belief in nature gods, and with the belief that the actions of oneself affect the nature of one's afterlife.

ParTI analysis of the *BHG* dataset

To test the generality of these findings, we analyzed an independent dataset of modern hunter-gatherer cultures[24] (Figure 3). Considering the first two principal components, which explain 33% of the variance of this dataset, we again find a distribution inside a triangle ($p<10^{-3}$) with three well-defined vertices (Figure 3A, Supplementary Information 5 and Table S2). For reasons discussed below, we assign the same three labels to these vertices. As with the *Pulotu* dataset, the traits show geographical trends (Figure 3B), and hence we performed regression adjusted for phylogenetic and spatial effects (Supplementary Information 6).

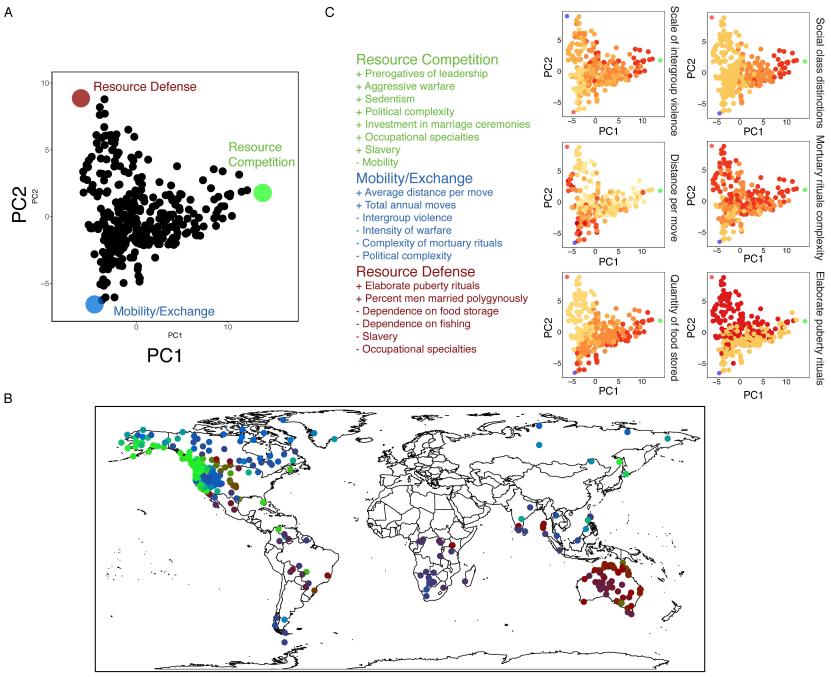

Figure 3. ParTI analysis of *BHG* dataset suggests three adaptive complexes. (A) Data plotted on the first two principal components of *BHG* dataset is well-described by a triangle ($p<10^{-3}$). The three vertices of the triangle are hypothesized to be adaptive complexes of traits for three tasks. (B) Cultures are color coded according to their relative distance from each vertex on a geographical map. (C) List of strongly enriched traits for each vertex. Sign (+/-) indicates positive or negative enrichment. Six of the enriched traits are displayed on the data distribution, with red (yellow) corresponding to a high (low) level of the trait. For example, social class distinctions are strongest close to the resource competition vertex, whereas elaborate puberty rites occur predominantly near the resource defense vertex.

Characterization of adaptive complexes for *BHG*

The hunter-gatherer cultures closest to the Resource Competition vertex are the stratified societies of the North-American Pacific Northwest, with strong enrichments for prerogatives of leadership, intense and aggressive warfare and political complexity, as well as sedentism (Figure 4C). As with the Austronesian cultures, the hunter-gatherers that are the closest to the Mobility/Exchange vertex come from areas with the lowest resource density – the arctic tundra and some deserts. This vertex is enriched with high mobility, low inter-group violence and low religious and political complexity. Last, the cultures closest to the Resource Defense vertex are Australian cultures from the relatively fertile Arnhem Land, and closeness to this vertex is associated with low dependence on food storage, elaborate male puberty rituals, and other traits that relate to marriage patterns.

We next asked whether the tasks of the three vertices found in the two datasets might be similar. This comparison is challenging due to the small overlap in traits between the two

239 datasets, and the differences in subsistence strategies. We note that in both datasets, the
240 Resource Competition vertex is enriched with traits that relate to territorial conquest and
241 social dominance and the cultures near the Mobility/Exchange vertex live in areas with lower
242 resource density. We tentatively conclude that the vertices might correspond to comparable
243 tasks, and use information from both datasets to provide an interpretation of these tasks.

244 **Economic defendability theory and the tasks**

245 We interpret the tasks of the three adaptive complexes using economic defendability
246 theory, a theory from behavioral ecology which relates variation in territorial behavior with
247 differences in resource density and predictability. This theory observes that only when a
248 resource is dense and predictable it is worthwhile to engage in costly behaviors to defend it.
249 Otherwise, other behaviors, such as mobility and exchange, will be preferred[33]. Economic
250 defendability was first used to explain the evolution of territorial systems in birds[32], and has
251 been applied to study-small scale human societies[33].

252 In agreement with economic defendability theory, the Mobility/Exchange vertex,
253 which is associated with cultures that live in areas with low resource density, is enriched with
254 lack of competitive cultural traits. The cultures nearest this vertex are highly mobile; their
255 reliance on trade or wage labor may compensate for poor and unpredictable resources;
256 prevalence of piercing may be explained by recent findings that extreme rituals promote pro-
257 sociality and inclusive social identity[36]; and their large ritual groups may reflect the need to
258 reinforce cultural identity in the face of dispersal[37]. For these reasons, we conclude that this
259 vertex is an adaptive complex of traits for the task of mobility and exchange.

260 Conversely, when resources are sufficiently dense and predictable, territorial
261 strategies should emerge. Territorial strategies require two separate tasks[34] – resource defense
262 and resource competition. The Resource Competition adaptive complex is enriched in both
263 datasets with socially competitive traits, which are associated with conquest and colonization,
264 whereas the Resource Defense adaptive complex is associated with traits that are more
265 cooperative.

266 Resource competition may become more important than resource defense when there
267 are strong resource gradients[38], unpredictable natural disasters[39] or due to population
268 pressure[31,40]. The enrichments for hierarchy-related traits near the Resource Competition
269 vertex may be due to the advantages of hierarchy for group-coordination[41] or for outgroup
270 exploitation[42].

271 As an example, the difference between the tasks can be illustrated by the headhunting
272 practices in two phylogenetically close cultures that lie on two sides of the same island:

Laboya from the western part of the island of Sumba, and *East Sumba* from its less fertile eastern part. *Laboya* lies close to the Resource Defense adaptive complex while *East Sumba* lies close to the Resource Competition adaptive complex. Both cultures used to practice headhunting (the practice of killing people to obtain their heads); however, in West Sumba the motivation for headhunting was reported to be defense of traditional territories, whereas in East Sumba its motivation was reported to be territorial expansion[43], in accordance with the proposed tasks for these adaptive complexes.

Discussion

In this study, we tested the hypothesis that tradeoffs are important for shaping cultural diversity, by using an approach from systems biology to infer tasks and tradeoffs and applying it multivariate datasets of cultural traits. We find a triangular geometrical structure of two independent cultural datasets, for Austronesian cultures and modern hunter-gatherers, in the space of traits. This triangle can be explained by a fundamental tradeoff between three tasks. We identify these tasks as mobility/exchange, resource defense and resource competition, and detect specific combinations of cultural traits that are predicted to be adaptive for each task, suggesting adaptive trait complexes. We conclude that tradeoffs may contribute to shaping some of the diversity of cultural traits.

The ParTI approach does not depend on the evolutionary mechanisms at play, nor does it suppose that a culture is perfectly adapted to its environment[44]. It provides a quantifiable, geometrical signature for generating hypotheses on the adaptive tasks of human social organization and cultural evolution.

The empty space around the triangle that describes the datasets corresponds to combinations of cultural traits that could a-priori have existed, but are not found in the data. For example, a combination of small ritual groups (as in resource defense vertex) together with reliance on trade/wage labour (as in mobility/exchange) is rare in the *Pulotu* dataset. In contrast, other combinations of traits often co-occur: such trait 'syndromes' are described by the vertexes of the triangle. ParTI, adjusted for phylogeny and spatial diffusion, explains both empty space and co-occurring traits based on tradeoffs between adaptive tasks.

ParTI might be useful to complement the methods of cultural evolutionary analysis. It overcomes some of the difficulties of existing approaches. One difficulty is in the interpretation of correlations between a given cultural trait and environmental factors[45]. For example, collectivist cultural values are correlated with pathogen prevalence, which led to the hypothesis they may represent an anti-pathogen defense strategy[46]. Interpreting such environmental associations is, however, often ambiguous, since they often relate to the

latitudinal gradient and may be explained by other factors[21]. ParTI uses multivariate data, rather than single traits, allowing stronger statistical inference and the ability to adjust for confounding geographical and phylogenetic factors.

Other approaches to model the function of cultural traits include optimality models from behavioral ecology[20,47] and co-evolutionary analyses[48]. Optimality models require information on costs and benefits that is not always available. Co-evolutionary models follow traits along phylogenetic trees, constructed for example from languages. They have been used to study associations such as the link between human sacrifice and social stratification[49] and the link between livestock and descent[50]. Such models, however, require strong phylogenetic signals and are not applicable to traits that have weak phylogenetic transmission.

The ParTI approach can, in principle, apply to any cross-cultural dataset, and thus may open new ways to test hypotheses on the tradeoffs that shape cultural adaptations. It provides a top-down way to provide hypotheses on the function of cultural traits and the trade-offs that shape cultural variation.

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