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ANTHROPOLOGY

EVOLUTION

Cultural macroevolution matters

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Evolutionary thinking can be applied to both cultural microevolution and macroevolution. However, much of the current literature focuses on cultural microevolution. In this article, we argue that the growing availability of large cross-cultural datasets facilitates the use of computational methods derived from evolutionary biology to answer broad-scale questions about the major transitions in human social organization. Biological methods can be extended to human cultural evolution. We illustrate this argument with examples drawn from our recent work on the roles of Big Gods and ritual human sacrifice in the evolution of large, stratified societies. These analyses show that, although the presence of Big Gods is correlated with the evolution of political complexity, in Austronesian cultures at least, they do not play a causal role in ratcheting up political complexity. In contrast, ritual human sacrifice does play a causal role in promoting and sustaining the evolution of stratified societies by maintaining and legitimizing the power of elites. We briefly discuss some common objections to the application of phylogenetic modeling to cultural evolution and argue that the use of these methods does not require a commitment to either gene-like cultural inheritance or to the view that cultures are like vertebrate species. We conclude that the careful application of these methods can substantially enhance the prospects of an evolutionary science of human history.

cultural evolution | macroevolution | phylogenetics | religion | Big Gods

Darwin's *On the Origin of the Species* ends with the poetic phrase, "From so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved" (1). The central challenge for evolutionary biology is to explain this diversity of endless forms. Evolutionary biologists tackle this task by studying both microevolution (changes in gene frequency within a population) and macroevolution (changes between species over much longer time periods). The aim is to have a mechanistic understanding of the evolution of biological diversity that integrates microlevel processes and macrolevel patterns. This work examines ways in which evolutionary thinking and methods can be extended into the realm of culture, extending the scope of biology to include questions that have traditionally been restricted to the humanities and social sciences. Human cultures also display a vast variety of most beautiful and most wonderful forms. We speak ~7,000 different languages, engage in hundreds of different religious practices, build many different types of houses, exploit different resources for subsistence, use numerous different kinship systems, and abide by a striking array of marital, sexual, and child-rearing norms (2). The cultural processes that produce such striking cultural diversity must be explained. The field of cultural evolution is currently beginning to blossom (Fig. 1). There is a new cultural evolution society, a proposed journal, and an inaugural conference (3). However, with a few notable exceptions (4), much of the current work on cultural evolution focuses on microevolutionary processes. For example, in Dan Sperber's influential book *Explaining Culture: A Naturalistic Approach* (5), cultural macroevolution rates only a passing mention on p. 2. More recently, in Lewens' (6) otherwise masterful analysis of current work on cultural evolution, macroevolutionary phenomena again fail to feature. This article is a plea—a plea for the importance of studying cultural macroevolution. Although we completely understand the need for elegant empirical work and appropriate models of cultural change within populations, we should never forget that the large-scale patterns of diversity between cultures also cry out for evolutionary analyses and explanation. The macro really matters.

Big(ish) Data and Need for Computational Methods

It is a cliché these days to talk about big data transforming the social sciences. However, clichés can be true. Certainly, there are a growing number of global comparative cultural and linguistic databases, such as D-PLACE (2), DRH (7), WALS (8), ASJP (9), and Phoible (10), as well as relatively large regional databases, such as the Austronesian Basic Vocabulary Database (11), SAILS (12), Chirilla (13), and Pulotu (14). Although these databases might not technically qualify as "big data," they are large enough to afford the application of the type of sophisticated computational methods that are often used in the biological sciences such as network analysis of reticulate evolution, epidemiological models, and phylogenetic comparative methods. These methods can be used to compare the relative importance of different factors in the distribution of traits, model the underlying dynamics of evolutionary change, and infer the history of traits. The combination of big(ish) data and computational methods has the potential to transform the social sciences and humanities by enabling powerful quantitative tests of hypotheses that would have previously only been analyzable in much more limited ways.

To illustrate the promise of this approach, we present a recent study by Botero et al. (15) titled, "The Ecology of Religious Beliefs," in which the authors examined the global distribution of moralizing high gods (MHGs)—supernatural beings who are claimed to have created or govern all reality, intervene in human affairs, and enforce or support human morality (sometimes referred to as "Big Gods"). These gods are central to the Abrahamic religions, which includes the two largest religious families in the world today, Christianity and Islam. Scholars have debated the social and physical environments in which MHGs most readily spread, and previous studies found rather contradictory results, with resource scarcity both positively and negatively associated with a belief in a MHG (16–18). These studies were limited by the use of crude metrics of ecology or indirect measures of

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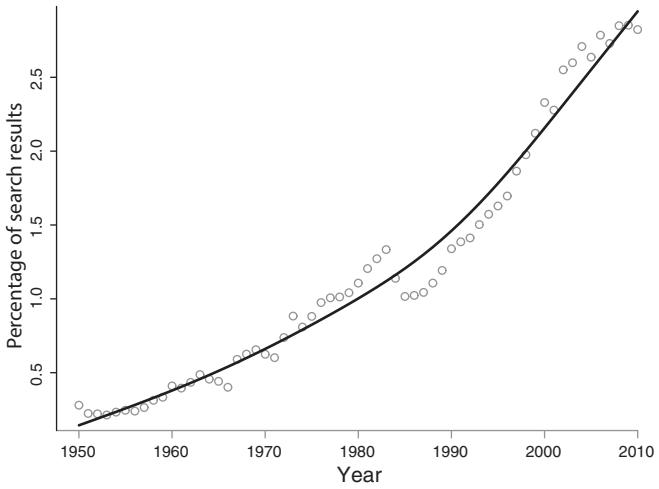

Fig. 1. Percentage of Google Scholar search results containing the term "cultural evolution" from 1950 to 2010.

agricultural potential, relatively small sample sizes, and a failure to account for the nonindependence of societies as a result of spatial proximity and common ancestry (19). Botero et al. (15) extracted fine-grained environmental data, as well as cultural, linguistic, and geographic information from the open-access D-PLACE database (https://d-place.org) (2). They used multimodel inference to simultaneously evaluate the effects of environmental variables, shared ancestry, geographic proximity, and social structures on belief in MHGs in 583 societies from around the globe. Generalized linear models and generalized linear mixed models were fitted in R (20) by using the lme4 (21) and MuMin (22) packages. The best-fitting models included spatial proximity, political complexity, animal husbandry, resource abundance, and resource stability. Belief in MHGs was more prevalent in societies from harsher environments and more likely in politically complex societies that had animal husbandry. Strikingly, this multimodel inference approach was able to predict the global distribution of belief in MHGs in a separate sample of cultures with an accuracy of 91%.

Major Transitions: Big Questions for Big(ish) Data

John Maynard Smith and Eörs Szathmáry's 1995 book, *The Major Transitions in Evolution* (23), is perhaps one of the most important and insightful contributions to evolutionary theory in the last 50 years. In this book, Maynard Smith and Szathmáry not only document fundamental changes in biological organization, such as the emergence of the genetic code, the origins of cells, the evolution of the eukaryotic cell, and multicellularity, they also show how these changes in biological organization change the way in which biological systems can evolve. The major transitions create entirely new evolutionary possibilities built upon new and more powerful ways of storing and transmitting information (24). According to Maynard Smith and Szathmáry (25), these transitions have at least five general properties:

1. Smaller entities form larger entities;
2. Smaller entities become differentiated as part of the larger entity;
3. The smaller entities are often unable to replicate in the absence of the larger entity;
4. The smaller entities can sometimes disrupt the development of the larger entity; and
5. New ways of transmitting information arise.

By themselves, large cross-cultural datasets and sophisticated computational methods are insufficient to create an exciting macroevolutionary science of human history. What is needed are big hypotheses and a powerful synthetic framework. We would like to suggest that much of the evolutionary thinking behind *The Major Transitions in Evolution* could be applied to cultural macroevolution (23).

Ten thousand years ago, most humans lived in small, kin-based, and relatively egalitarian groups (26). Today, we live in colossal nation states with distantly related members, complex hierarchical organization, and huge social inequality. Although kin selection and reciprocity explain a great deal of cooperation in the animal kingdom, these mechanisms break down in modern societies because the sheer scale of modern societies means that people can be anonymous and only distantly biologically related (27). The challenge is to explain the cultural forces that enabled this major transition in the size and complexity of human social groups to occur.

The potential of religious beliefs and practices to bind together social groups has long been recognized (28), although these functions have only recently been considered from an explicitly evolutionary perspective (29–31). One prominent theory is that belief in supernatural punishment, particularly by powerful and omnipotent Big Gods, inhibits selfishness and increases cooperation among adherents (32–34). The intuitive idea is that if people believe a punishing and moral supernatural agent is monitoring them, they are more likely to behave themselves. By facilitating cooperation in large groups of nonkin, beliefs in supernatural punishment are thought to have played a causal role in the emergence of large, complex human societies (33, 35, 36). It is crucial to emphasize that, at least as it was initially formulated, this hypothesis was both causal and directional. Big Gods were needed to make big societies. For example:

> It is no coincidence that the world is now dominated by a few great monotheisms, and that much human behaviour is influenced by the belief in a few high gods. To achieve a civilization of this scale, it was necessary to invent them (36);

and

> One reason societies were able to develop cultural complexity in the first place is partly on account of the cooperative benefits attained through a belief in moralizing gods (35).

In support of the Supernatural Punishment Hypothesis, a number of cross-cultural studies have shown that belief in MHGs is positively correlated with a range of measures of social complexity, such as political hierarchy, agriculture, and taxation systems (18, 35). On the face of it, the cross-cultural evidence for the Supernatural Punishment Hypothesis appears compelling. However, these studies have a number of important limitations (37). First, these studies do not actually get at the direction of causality. Although one possible explanation for these results is that MHGs facilitate social complexity, another is that social complexity makes cultures more likely to adopt MHGs. Second, these studies are ether based on a single dataset called the Ethnographic Atlas or a subset of this dataset known as the Standard Cross-Cultural Sample (17, 18, 35, 38). The MHGs in these datasets are almost all derived from the closely related family of Abrahamic religions—Christianity, Judaism, and Islam (37). These religions share a wide range of features, such as providing a universal rather than ethnocentric doctrine and encouraging fertility, and it is not clear whether it is an MHG specifically or some other part of these religions that is related to social complexity (37, 39). Third, cultures often inherit traits such as language, customs, oral traditions, and social norms from their ancestors (19). These relationships between cultures mean that cultures cannot be treated as statistically independent–a problem famously first pointed out by Francis Galton (40, 41).

The studies mentioned above do not adequately account for Galton's Problem, so the correlation observed between the presence of MHGs and social complexity might merely arise because of the historical relationships between cultures (42). Thus, to rigorously test hypotheses about the role of MHGs in driving the major transitions in human history, we need data from cultures with non-Abrahamic religions, as well as methods that avoid Galton's Problem and can explicitly test causal predictions.

Phylogenetic methods have revolutionized the field of evolutionary biology (43). These methods solve Galton's Problem by explicitly estimating ancestral state changes on phylogenetic trees (19, 41). Thus, there is no overcounting or undercounting of evolutionary events. Phylogenetic methods have recently been used to make inferences about things such as the ancestral state of postmarital residence patterns in Austronesian cultures (44), the evolution of political complexity (45), the effects of cultural ancestry on deforestation (46), and the links between cattle and matrilinity (47). Mark Pagel and Andrew Meade introduced a method called "Discrete" in the program BayesTraits that models the evolution of two binary traits and tests between dependent and independent models of evolution (48, 49). In an independent model, the gains and losses of each trait are modeled separately from each other (Fig. 2*A*). In the dependent model, the rate at which a trait is gained or lost depends on the state of the other trait, as would be expected if there is a causal relationship between traits (Fig. 2 *B* and *C*). This approach gets at the direction of causality by inferring the temporal order that traits tend to arise and the effects they have on one another (49).

Using this approach and data from the Pulotu database (14, 49), we recently tested a series of hypotheses about the role of religion in the emergence of social complexity (14, 50, 51). The Pulotu database contains quantitative variables documenting the traditional religious beliefs and practices as well as the social organization of 106 Austronesian cultures. Special care was taken in the coding of these data to ensure that, as far as possible, the coding reflected the state of the culture before conversion to major world religions and colonization (14). Previously published language-based phylogenies were used as a proxy for the population history of these cultures (52). These trees fit remarkably well with archaeological evidence that shows Austronesian-speaking cultures were some of the greatest ocean voyagers in human history, sailing from their homeland in Taiwan to settle on islands ranging in size from the 0.4-km^2 island of Anuta up to the 785,000-km^2 continental island of New Guinea (14, 53, 54). The archaeological, genetic, and linguistic evidence suggests that this expansion started ∼5,000 y ago and spread in a series of expansion pulses and pauses through Island South East Asia and the Pacific (52–55). The cultures that evolved on these islands ranged from small kin-based groups, such as the Berawan (56), up to federated kingdoms, such as Southern Toraja (57). Population sizes ranged from ∼200 people on Anuta (58) to approximately half a million people in the case of the Merina of Madagascar (59). No less diverse were their religious systems, with supernatural beliefs including anthropomorphic, animistic, and nature deities, and religious rituals ranging in scale from humble personal offerings to multiday community-wide festivals (14). Because Austronesian cultures were some of the last cultures in the world to have contact with major world religions, and their traditional beliefs were well documented, they provide an ideal sample for testing theories about the role of religion in the emergence of social complexity.

We ran two series of analyses to test the Supernatural Punishment Hypothesis (50). In the first, we tested the effect of Broad Supernatural Punishment on the evolution of political complexity. Agents counted in this test included a wide range of punishing and morally concerned supernatural agents, such as ancestral spirits, natural spirits (e.g., forest and sky gods), and mythical heroes, in addition to MHGs (14). Belief in Broad Supernatural Punishment was found in just over two-thirds of the cultures sampled. We found modest support for the coevolution of Broad Supernatural Punishment and political complexity, with Broad Supernatural Punishment facilitating the rise of political complexity, but not helping to sustain it. In the second series of analyses, we tested whether the specific belief in MHGs coevolved with political complexity. We were surprised to find evidence of MHGs in just 6 of the 96 traditional Austronesian cultures we studied. Although our analyses suggested that MHGs coevolved with political complexity, instead of MHGs driving political complexity, our results indicated that MHGs tended to be gained after political complexity had already emerged (Fig. 2*C*). Our analyses suggested that these MHGs had been gained only recently, and most of these MHGs occurred in regions where there had been early contact with Muslim traders. Although we

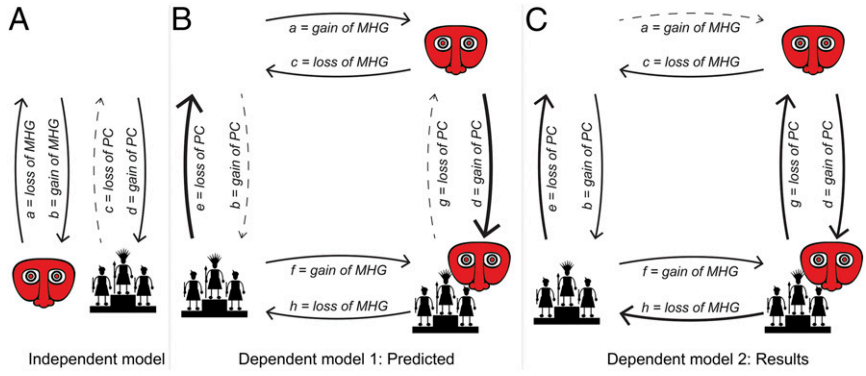

Fig. 2. An independent model (*A*) of evolution alongside the dependent model predicted by the Supernatural Punishment Hypothesis (*B*) and the dependent model resulting from analyses of traditional Austronesian cultures (*C*). The red figure represents the presence of a MHG, and the black figure represents the presence of political complexity (PC). Arrows indicate the rates of change between states, and the width of the arrows are proportional to the size of the transition rates. (*A*) In independent models of evolution, the rate at which each trait is gained or lost is independent of the state of the other trait. In this example, cultures are more likely to gain PC than to lose it (rate *c* is lower than rate *d*). (*B*) In dependent models of evolution, the rate at which each trait is gained and lost can be dependent on the state of the other. In the model predicted by the Supernatural Punishment Hypothesis, the rate at which PC is gained is higher when a MHG is present (rate *d*) than when it is absent (rate *b*), and the rate at which PC is lost is lower when an MHG is present (rate *g*) than when an MHG is absent (rate *e*). (*C*) The resulting models from our analyses suggested that MHGs had little effect on the gain and loss of PC, but that MHGs were rarely gained in cultures without PC (rate *a* is lower than rate *f*).

excluded all clear cases of direct borrowings from Abrahamic religions, it is likely that the concept of a MHG was subtly borrowed and transferred to the names of indigenous deities (60).

Defenders of the Big Gods hypothesis might argue that, for some reason, the Austronesian cultures do not reflect the role MHGs played in the emergence of social complexity in other regions of the world. However, a closer examination of previous cross-cultural studies suggests otherwise. Of the 40 MHGs in the Standard Cross Cultural Sample, 32 are of Christian or Islamic origin, and the remaining 8 are either other Abrahamic religions or plausibly influenced by them (37). The Abrahamic religions arose ~3,000 y ago, long after humans had begun forming large, sedentary, and complexly organized societies (26). Although there is a substantial body of experimental research showing that Abrahamic MHGs can increase cooperation within groups (61), the timing of their origin means that they cannot explain at least the initial emergence of social complexity in human history. This finding tells us that microlevel processes observed in contemporary cultures do not necessarily explain the macroevolutionary patterns observed in human history.

An alternative vein of scholarship has focused on the darker role of religion in human social life (62, 63). Archaeological, historical, and ethnographic records reveal that in early societies religious and political authority often overlapped (26), providing ample opportunities for elites to use religious systems toward their own ends. As a result, religious narratives in early human societies often legitimize the authority of those in power and involve rituals that benefit the elite at the expense of underclasses (64). A particularly gruesome example is the practice of ritualized human sacrifice that occurred in early human societies throughout the world (64–68). According to the Social Control Hypothesis (64, 66, 68), ritualized human sacrifice was used by social elites as a religiously sanctioned means of terrifying underclasses into obedience.

To test the Social Control Hypothesis, we went back to the Pulotu database (14), coded variables on human sacrifice and social stratification, and tested for their coevolution (51). The term "social stratification" refers to inherited differences in wealth and status and is thought to have been one of the earliest forms of hierarchical structuring to emerge in human history (26). We found human sacrifice to have been remarkably common in traditional cultures, occurring in almost half of those sampled (51). Typically, social elites orchestrated the sacrifices, with social underclasses becoming the victims. The results of our analyses showed that human sacrifice coevolved with social stratification and functioned to stabilize social inequality in general, as well as facilitated the emergence of rigid class systems (Fig. 3). This result does not imply that human sacrifice was necessarily functional for the whole group, nor that it would have these effects in modern societies, which have developed more sophisticated methods of sustaining social inequality. What our results do show is that ritual human sacrifice was used by social elites as a tool to maintain their social standing in the early stages of social complexity.

Overextension of Biological Metaphors and Methods?

The famous evolutionary biologist Richard Lewontin often liked to cite Rosenblueth and Wiener's quip that, "The price of metaphor is eternal vigilance" (69). One of the things that Lewontin is particularly skeptical about is the metaphorical extension of evolutionary ideas to cultural history (70, 71). Part of this skepticism is driven by his opposition to Dawkins' meme concept (72). Fracchia and Lewontin write (70):

> But, unlike genes, memes are not entities with an existence independent of the theory. They are a mental construct whose only defined property is to fill in the gap in an elaborate metaphor.

However, Lewontin's own three central principles for systems to evolve by natural selection (phenotypic variation, differential fitness, and inheritance) are satisfied by cultural systems (4, 73). As Henrich and Boyd have shown, adaptive cultural evolution does not require replicator-like inheritance systems (74).

There is, however, another line of skepticism that is sometimes directed against attempts to apply phylogenetic methods to cultural evolution. Lewontin's former colleague, Steven Jay Gould (75), put this view with characteristic vigor:

> Human cultural evolution proceeds along paths outstandingly different from the ways of genetic change… Biological evolution is constantly diverging; once lineages become separate, they cannot amalgamate (except in producing news species by hybridization—a process that occurs very rarely in animals). Trees are correct topologies of biological evolution… In human cultural evolution, on the other hand, transmission and anastomosis are rampant. Five minutes with a wheel, a snowshoe, a bobbin, or a bow and arrow may allow an artisan of one culture to capture a major achievement of another.

Although Gould may have hugely overestimated how easy it is to reverse-engineer the manufacture of these items, the critique of cultural phylogenetics has not gone away. Recently, Norenzayan et al. (76) stated:

> We caution against rushing to embrace analytical techniques imported from genetic evolution – used to reconstruct species phylogenies – to cultural evolution. Cultural evolution is in some crucial respects unlike genetic evolution… Species, for example, are not subject to intergroup competition that creates massive and directed horizontal transmission of only some traits. Therefore, we think the first step should be to benchmark phylogenetic techniques to cultural history using known historical cases.

For the sake of clarity, we should be clear that we are not advocating the blanket adoption of phylogenetics to all cultural phenomena. So, let us look more closely at what the legitimate concerns may or may not be. The statements above could be boiled down to four linked, but logically separate, claims:

1. Culture evolves differently from biology. Biological evolution is treelike, but in culture reticulation rules.
2. Cultures are not (vertebrate) species. Different aspects of culture will have quite different histories.
3. The estimation of phylogenetic trees will be biased by horizontal transmission.
4. The accuracy of cultural phylogenies has not been validated.

The first claim displays a shocking lack of knowledge of biology and human culture. There is a great deal of biology that does not fit tidily on the "tree of life." Indeed, the tree of life has been mocked as the "tree of 1%" (77). A very significant amount of cross-lineage transfer occurs in biological evolution, especially in microbes (78). Mallet (79) estimated that there is hybridization in ~10% of animal and 25% of plant species. Dagan and Martin's (80) analysis of 190 prokaryotic genomes suggests that horizontal gene transfer has affected at least two-thirds of >57,000 gene families.

In the literature on cultural microevolution, there is evidence that the majority of social learning occurs between members of the same population, but the relative importance of parent-to-offspring and peer-to-peer social learning is debated (81–84). What matters for the application of phylogenetic methods are the resulting macroevolutionary patterns. Given that social learning occurs predominantly within a population, both peer-to-peer and parent-to-offspring learning can result in vertical transmission at the macroevolutionary level. The relative importance of vertical and horizontal transmission between populations is likely to vary across domains of culture, world regions, and periods of history. For example, the design of the internal combustion engine has been borrowed between cultural lineages. Conversely, basic vocabulary items, such as terms for hand and eye, lower numerals, and kinship terms show clear evidence of vertical transmission down cultural lineages (85).

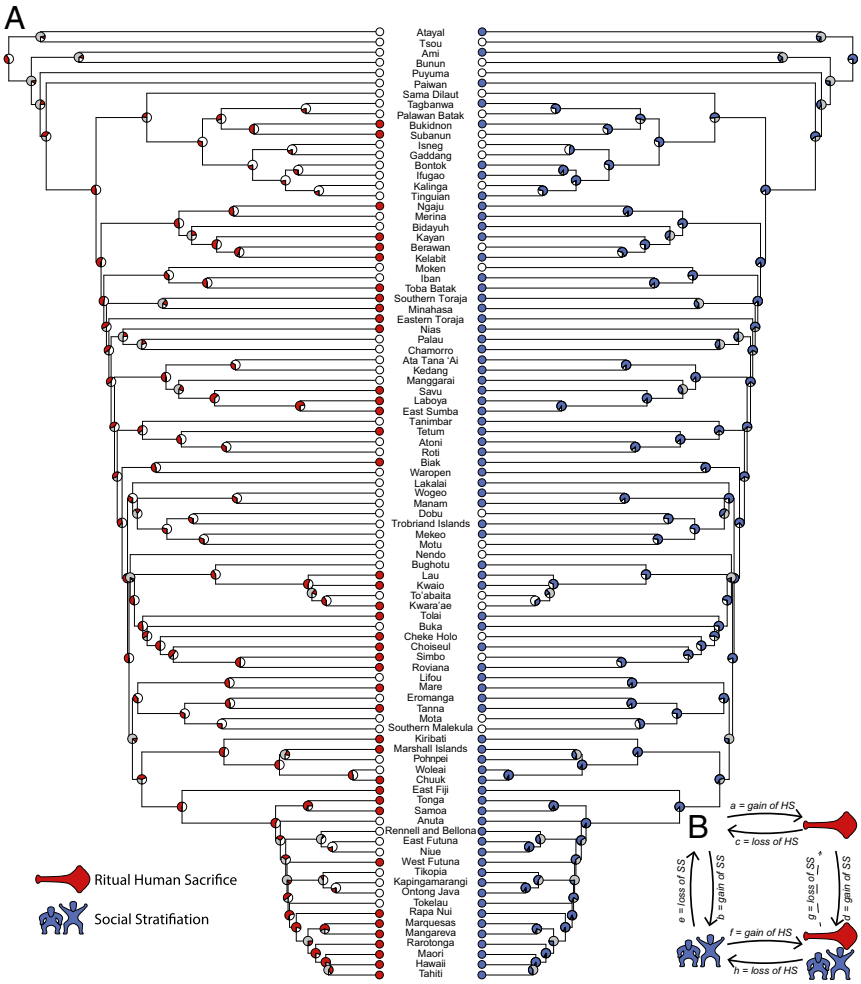

Fig. 3. (*A*) Ancestral state reconstruction of human sacrifice and social stratification on a maximum clade credibility consensus tree of 93 Austronesian languages. The circles at the tips of the tree represent the known traditional states of cultures, and the circles found across the nodes of the tree represent the state of prehistoric cultures inferred by a Markov chain Monte Carlo analysis in BayesTraits. In the analysis, 4,200 of the most likely possible trees were used, and the consensus tree is a summary of these trees for illustrative purposes. The gray at each of the internal nodes represents the proportion of trees sampled without this node and provides an indication of phylogenetic uncertainty. (*B*) The resulting dependent model shows that cultures with ritualized human sacrifice were less likely to lose social stratification than those that lacked human sacrifice (rate *g* is lower than rate *e*). Adapted from ref. 51.

The second claim is more sensible, but does not undermine the use of phylogenetic methods. If anything, it points out an important role for their use—to assess the coherence of difference aspects of culture. In their book chapter, "Are Cultural Phylogenies Possible?", Boyd et al. (86) describe a range of positions along a continuum on the question of how integrated cultural histories are: (*i*) Cultures are tightly integrated like vertebrate species; (*ii*) cultures contain a core of traditions that are tightly linked and vertically transmitted, with peripheral aspects that are less cohesive and marked by frequent borrowing; (*iii*) cultures contain some aspects that are bound together, but there are no core traditions; and (*iv*) cultures are collections of ephemeral entities. Just as biologists talk about "every gene having its own history," and have developed methods to map these gene genealogies on to a species phylogeny, so cultural phylogenetists could construct trees for different aspects of culture and evaluate their fit with population history (87, 88). For example, genealogies of religious beliefs, material culture, kinship systems, music genres, and styles of art could be mapped and compared with language-based cultural histories. Phylogenetic methods make the traditional social science debate about the extent to which a culture is an integrated whole testable.

The third objection—that the estimation of cultural phylogenies will be biased by horizontal transmission—is a quantitative issue that can be evaluated by simulation modeling. Greenhill et al. (89) simulated language phylogenies with different tree topologies, different borrowing scenarios, and different levels of borrowing. The results show that tree topologies constructed with Bayesian phylogenetic methods are robust to realistic levels of borrowing. Inferences about divergence dates were slightly less robust and showed a tendency to underestimate dates.

The final objection—have inferences from cultural phylogenetics been validated?—is a fair enough concern, but one that applies to much of computational biology, and indeed the extrapolation of laboratory studies to the field. In brief, we will point out that the Austronesian languages phylogenies built from basic vocabulary fit strikingly well with both archaeological (55) and recent genetic data (90, 91), both in terms of the sequence and the timing of the Austronesian expansion.

Conclusion

In the coming years, more quantitative phylogenies for the major language families will be published, and the number and richness of comparative cultural databases will undoubtedly grow (7, 92).

The series of studies we have discussed in this work illustrate how causal theories about the emergence of major transitions in human social organization can be tested with the combination of large quantitative cross-cultural data and computational phylogenetic methods. We do not claim that these methods are appropriate for all questions and for all spatial and temporal time scales in cultural evolution. Instead, we suggest that, when they are used carefully in cases where there is clear historical signal, such as the Austronesian or Bantu expansions (52, 93), and where the inferences are triangulated with other lines of evidence (94), then they can make an important contribution to our understanding of cultural macroevolution. They can even be used to predict political and economic changes (95). Although there is much still to be done to integrate microlevel processes and macrolevel patterns, the macro not only matters, it is tractable.

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