

Ritual human sacrifice promoted and sustained the evolution of stratified societies

Joseph Watts¹, Oliver Sheehan^{1,2}, Quentin D. Atkinson^{1,2}, Joseph Bulbulia³ & Russell D. Gray^{1,2,4,5}

Evidence for human sacrifice is found throughout the archaeological record of early civilizations¹, the ethnographic records of indigenous world cultures^{2–5}, and the texts of the most prolific contemporary religions⁶. According to the social control hypothesis^{2,7,8}, human sacrifice legitimizes political authority and social class systems, functioning to stabilize such social stratification. Support for the social control hypothesis is largely limited to historical anecdotes of human sacrifice^{2,8}, where the causal claims have not been subject to rigorous quantitative cross-cultural tests. Here we test the social control hypothesis by applying Bayesian phylogenetic methods to a geographically and socially diverse sample of 93 traditional Austronesian cultures. We find strong support for models in which human sacrifice stabilizes social stratification once stratification has arisen, and promotes a shift to strictly inherited class systems. Whilst evolutionary theories of religion have focused on the functionality of prosocial and moral beliefs^{9,10}, our results reveal a darker link between religion and the evolution of modern hierarchical societies^{11,12}.

Human sacrifice—the deliberate and ritualized killing of an individual in order to please or placate supernatural beings—is known to have occurred in early Germanic, Arab, Turkic, Inuit, American, Austronesian, African, Chinese and Japanese cultures¹. Speculation about the potential functionality of human sacrifice dates back to at least the beginning of the European colonization of Central America 500 years ago³, and has been the subject of enduring debate across the humanities^{2,13,14}, social sciences^{1,8,15,16} and biological sciences^{17,18} ever since. The practice has been conjectured to act as a form of social catharsis¹³, a justification for political conflicts¹⁵, and, when combined with cannibalism, a means of overcoming protein shortages¹⁶. Political theorists have long argued that effective political authority in class-stratified societies requires legitimizing mechanisms^{12,19}, an idea which evolutionary scholars have recently endorsed^{11,20}. According to the social control hypothesis, human sacrifice legitimizes class-based power distinctions by combining displays of ultimate authority—the taking of a life—with supernatural justifications that sanctify authority as divinely ordained^{2,8,13}. Social stratification is thought to have been one of the earliest forms of institutionalized leadership to emerge in human cultures, giving rise to kingdoms, monarchies and modern political states^{20,21}. Existing support for the social control hypothesis is based on anecdotal descriptions of cultures^{2,8,15}, and one quantitative cross-cultural study that found an association between human sacrifice and measures of social and political complexity⁷. However, this study used a sample that contained just seven cultures that practiced human sacrifice, did not control for the non-independence of cultures^{7,22}, and was unable to infer the direction of causality between human sacrifice and social stratification²³.

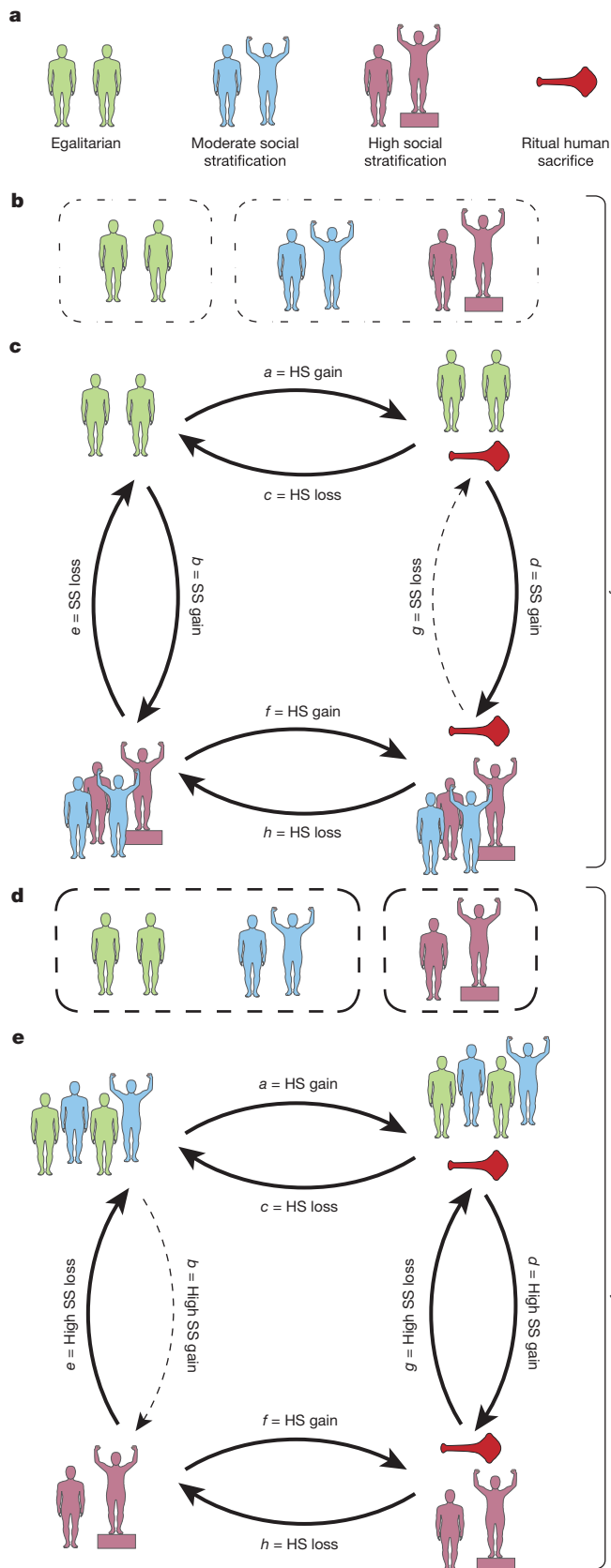
Here we test the social control hypothesis with a Bayesian phylogenetic analysis of 93 traditional Austronesian cultures from the Pulotu database²⁴. Phylogenetic methods enable us to account for the

common ancestry of cultures²⁴, test for patterns of coevolution^{10,25}, and infer the direction of causality based on the order that traits evolve in²³. Austronesian cultures have been described as a natural laboratory for cross-cultural research due to the diversity of environments they inhabit and cultural features they have evolved²⁶. They inhabit environments ranging from tiny atolls to continents²⁴, and their social structures ranged from small egalitarian, kin-based societies such as the Dobuans²⁴, to large, complex polities such as the Hawaiians²⁷. From their ancestral homeland in Taiwan, Austronesian cultures spread west to Madagascar, east to Rapa Nui, and south to New Zealand—a region covering over half the world's longitude and one-third of its latitude²⁴. Their religious beliefs and practices were remarkably diverse^{3,4,10}, and the practice of human sacrifice was widespread throughout traditional Austronesian cultures. Common occasions for human sacrifice in these societies included the breach of taboo or custom⁴, the funeral of an important chief²⁷, and the consecration of a newly built house or boat³. Ethnographic descriptions highlight that the sacrificial victims were typically of low social status, such as slaves, and the instigators were of high social status, such as priests and chiefs^{3,4,27}. The methods of sacrifice included burning, drowning, strangulation, bludgeoning, burial, being crushed under a newly built canoe, being cut to pieces, as well as being rolled off the roof of a house and then decapitated^{3,4,27}.

For each culture in our sample, we recorded the presence or absence of human sacrifice, and coded the level of social stratification. Cultures that lacked inherited differences in wealth and status were defined as lacking social stratification, and were coded as egalitarian. Cultures were coded as moderately stratified if there were inherited differences in wealth and social position with the potential for status change within a generation, and highly stratified if there were inherited difference in wealth and social position with little or no possibility of status change within a generation (further details are provided in the Methods section). The social control hypothesis predicts that human sacrifice (i) co-evolves with social stratification, (ii) increases the chance of a culture gaining social stratification, and (iii) reduces the chance of a culture losing social stratification once stratification has arisen. Though the social control hypothesis could potentially apply to stratified societies in general⁸, the hypothesis is based on descriptions of human sacrifice in highly stratified societies such as the Aztecs². Here we perform two series of analyses, the first to test the effects of human sacrifice on the evolution of social stratification in general, and the second to test the effects of human sacrifice on the evolution of high social stratification (Fig. 1c, e).

We found that the extent of social stratification, as well as the presence of human sacrifice, varied throughout a wide range of geographic regions and cultural groups (Fig. 2 and Extended Data Fig. 1). Evidence of human sacrifice was observed in 40 of the 93 cultures sampled (43%). Human sacrifice was practiced in 5 of the 20 egalitarian societies (25%), 17 of the 46 moderately stratified societies (37%), and 18 of the 27 highly stratified societies (67%) sampled.

¹School of Psychology, University of Auckland, Auckland 1142, New Zealand. ²Max Planck Institute for the Science of Human History, Jena 07743, Germany. ³School of Art History, Classics and Religious Studies, Victoria University of Wellington, Wellington 6014, New Zealand. ⁴Research School of the Social Sciences, Australian National University, Canberra 2601, Australia. ⁵Allan Wilson Centre for Molecular Ecology and Evolution, Palmerston North 4442, New Zealand.



In our first series of analyses, we grouped moderate and high stratification together, referred to hereafter as ‘social stratification’ (Fig. 1b). To test for the co-evolution of human sacrifice and social stratification, we compared the posterior distribution of models in which human sacrifice and social stratification evolve independently of one another

Figure 1 | Summary of the two series of analyses performed in this study. **a**, Key of the images used to represent social stratification and human sacrifice. **b**, In the first series of analyses, moderately and highly stratified societies cultures were grouped together to test for the co-evolution of human sacrifice with social stratification in general. **c**, Unconstrained dependent model of the co-evolution of human sacrifice (HS) and social stratification (SS) in general. The thicknesses of the arrows are proportional to the rates of change between states. **d**, In the second series of analyses, egalitarian and moderately stratified societies were grouped together to specifically test for the co-evolution of human sacrifice with high social stratification. **e**, Unconstrained dependent model of the co-evolution of human sacrifice (HS) and high social stratification (high SS). The thicknesses of arrows are proportional to the rates of change between states.

with models in which the two traits co-evolve such that the probability of a change in one trait is dependent on the value of the other trait²³. We found substantial support for the models in the dependent analyses, in which human sacrifice can co-evolve with social stratification, compared with the models in the independent analyses (Bayes factor (BF) = 3.78). This indicates that human sacrifice co-evolved with social stratification. We then performed two additional constrained analyses to test whether human sacrifice functioned to drive and stabilize the evolution of social stratification, as the social control hypothesis predicts. In the first constrained analysis, cultures with and without human sacrifice were forced to have an equal chance of losing social stratification (rates e and g in Fig. 1c were set to be equal). The resulting models fitted substantially more poorly than the unconstrained dependent analyses (BF = 2.30), and did not fit substantially better than the models in the independent analysis (BF = 1.48). This indicates that human sacrifice affects the rate at which cultures lose social stratification. The unconstrained dependent model shows that cultures with human sacrifice were less likely to lose social stratification than were cultures that lacked human sacrifice (in Fig. 1c rate e is higher than rate g). In the second constrained analysis, the rate at which cultures with and without human sacrifice gained social stratification was forced to be equal (rates b and d in Fig. 1c were set to be equal). The resulting models were substantially more likely than were models in the independent analysis (BF = 4.68), and slightly more likely than models in the unconstrained dependent analysis, though not substantially so (BF = 0.60). Together these results indicate that human sacrifice functioned to stabilize social stratification once it had arisen, but did not affect whether egalitarian cultures gained social stratification (in Fig. 1c, rate e is higher than rate g).

In our second series of analyses, we used the same approach to test whether human sacrifice co-evolves with high social stratification specifically. In this series, we grouped egalitarian and moderately stratified societies together (Fig. 1d). We found strong support for the models in the dependent analyses over the models in the independent analyses (BF = 6.04), indicating that human sacrifice has co-evolved with high social stratification. To test the prediction that human sacrifice functions to stabilize and drive high social stratification, we performed the same sequence of constrained analyses as previously described for social stratification in general. In the first constrained analysis, cultures with and without human sacrifice were forced to have an equal chance of losing high social stratification (rates e and g in Fig. 1e were equal). The resulting models were more likely than those in the independent analysis (BF = 6.96) and the unconstrained dependent analysis (BF = 0.92), though the difference was only substantial in the case of the former. This indicates that the presence of human sacrifice is not associated with a change in the rate at which highly stratified cultures become less stratified. The second analysis was constrained so that cultures with and without human sacrifice were forced to have an equal chance of gaining high social stratification (rates b and d in Fig. 1e are equal). The resulting models were substantially less likely than were the models in the unconstrained dependent analysis (BF = 4.70), and

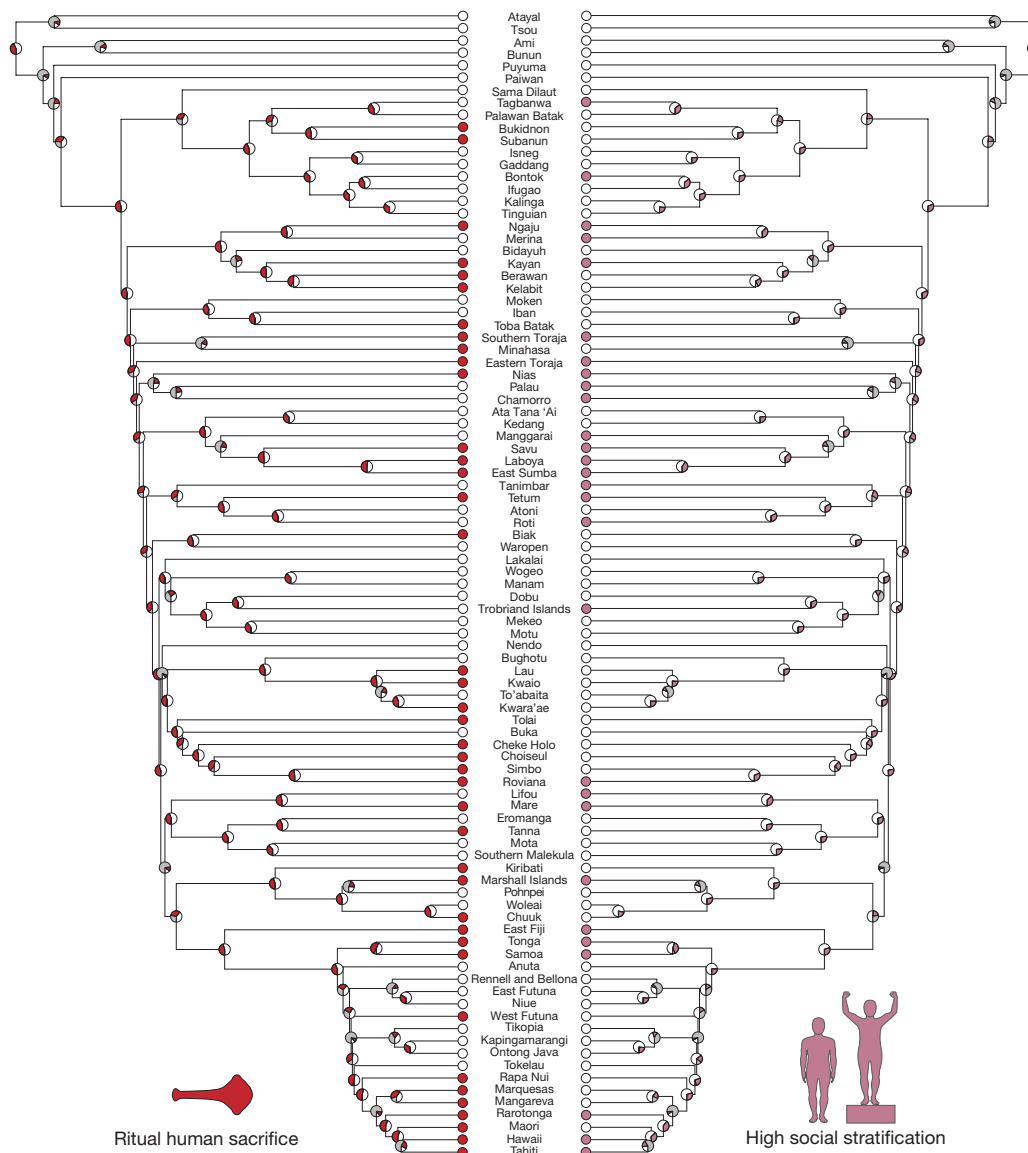


Figure 2 | Phylogenetic distribution of human sacrifice and high social stratification in Austronesia. Ancestral state reconstruction of human sacrifice and high social stratification on a maximum clade credibility consensus tree of 93 Austronesian languages. This analysis was run for

2×10^9 iterations and replicated three times. Pie charts at the nodes represent the probable ancestral state in the unconstrained dependent reversible-jump Markov chain Monte Carlo²³ analysis. Grey represents the proportion of our sample of 4,200 trees in which that node is absent.

slightly less likely than the models in the independent analysis, though not substantially so ($BF = 1.34$). The results from our second series of analyses indicates that human sacrifice increased the rate at which cultures with human sacrifice gain high social stratification, but did not function to stabilize high social stratification once it had arisen (in Fig. 1e, rate d is higher than rate b).

Taken together, our results provide strong evidence for the claim that human sacrifice played a powerful role in the construction and maintenance of stratified societies. Though human sacrifice was practiced in the majority of highly stratified societies in our sample, it was scarce in egalitarian societies, and we find that its effect depended on the level of stratification. Specifically, human sacrifice substantially increased the chances of high social stratification arising and prevented the loss of social stratification once it had arisen, yet was not found to increase social stratification in egalitarian societies. This is consistent with historical accounts that speculate that in order for human sacrifice to be exploited by social elites, there must first be social elites to exploit it^{2,8}. In our ancestral reconstructions Proto-Austronesian culture is inferred to have had some level of social stratification (Extended Fig. 1), but

not high social stratification (Fig. 2), and the most common changes inferred across our trees were the loss of social stratification in general, and the gain in high social stratification. We caution that the lack of support we find for human sacrifice sustaining high social stratification may be due to high social stratification having been rarely lost in the history of Austronesian cultures.

Experimental research indicates that while social inequality may foster group decision-making and efficiency²⁸, power hierarchies become unstable when they lack sanctioning status²⁹. In Austronesian cultures human sacrifice was used to punish taboo violations⁴, demoralise underclasses²⁷, mark class boundaries³, and instil fear of social elites²⁷ — proving a wide range of potential mechanisms for maintaining and building social control. Throughout human history the practice of human sacrifice was often used by social elites as a display of power^{2,8}, intended to instil fear of the secular and supernatural consequences of transgressing ruling authority. While there are many factors that help build and sustain social stratification, human sacrifice may be a particularly effective means of maintaining and building social control because it minimizes the potential of retaliation by eliminating the

victim, and shifts the agent believed to be ultimately responsible to the realm of the supernatural¹³.

Religion has long been proposed to play a functional role in society¹⁹, and is commonly claimed to underpin morality. Recent evolutionary theories of religion have focused on the potential of pro-social and moral religious beliefs to increase cooperation^{9,10}. Our findings suggest that religious rituals also played a darker role in the evolution of modern complex societies. In traditional Austronesian cultures there was substantial religious and political overlap, and ritualised human sacrifice may have been co-opted by elites as a divinely sanctioned means of social control^{11,12,30}. The approach adopted in this paper demonstrates the way causal hypotheses about major transitions in human social organization can be tested by combining computational models and language phylogenies with a wealth of cultural and historical data. Unpalatable as it might be, our results suggest that ritual killing helped humans transition from the small egalitarian groups of our ancestors, to the large stratified societies we live in today.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is available in the online version of the paper.

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Author Contributions J.W. designed the study with Q.D.A., J.B. and R.D.G. J.W. and O.S. jointly created and coded the variables. J.W. performed the analyses with input from Q.D.A. and R.D.G. J.W., O.S., Q.D.A., J.B. and R.D.G. reviewed the results and wrote the paper.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to J.W. (me@josephwatts.org).

METHODS

Data reporting. No statistical methods were used to predetermine sample size. The investigators were not blinded during experiments and outcome assessment.

Data and coding. Human sacrifice was coded as present (present = 1) if there was evidence that members of the culture practiced the ritual killing of human beings, in a non-military context, for the sole or primary purpose of pleasing or appeasing a supernatural agent. Deaths that occurred during raids on enemy cultures, or non-ritual murders that resulted from interpersonal conflicts, were not considered to be human sacrifice. Human sacrifice was coded as absent (absent = 0) if ethnographic sources explicitly stated that human sacrifice was not practiced, or if there was no evidence of human sacrifice from a substantial description of the culture's religious practices. Building on an established classification system of social stratification in Polynesian cultures³¹, we grouped Austronesian cultures into one of three categories. Cultures were coded as egalitarian (egalitarian = 1) if there was minimal or no potential for wealth and/or status to be inherited between generations. Cultures were coded as having moderate social stratification (moderate social stratification = 2) if pronounced intergenerational differences in wealth and/or status existed between social groups, but one or more of the following conditions was met: (a) social mobility was not restricted at any level, (b) differences in status and/or wealth were not associated with pronounced differences in living standards, and/or (c) the social groups in question were not clearly delineated. Finally, cultures were coded as highly stratified (high social stratification = 3) if pronounced intergenerational differences in wealth and/or status, associated with pronounced differences in living standards, existed between clearly delineated social groups and social mobility between two or more of the groups was restricted.

Cultures were the units of analysis in this study. We coded all the cultures from the Pulotu database²⁴ for which data on human sacrifice and social stratification were available, and that could be linked to a language on a phylogenetic tree²⁵. Pulotu contains a diverse and broadly representative sample of Austronesian speaking cultures and information was collected on the traditional states of these cultures from periodicals, books and encyclopaedias (Supplementary Table 1). We coded cultures as they were before substantial influence by industrialized cultures and major world religions. This influence occurred through modernizing processes such as colonization, missionization, and trade. Sampling traditional Austronesian cultures has the advantages of reducing the effects of cultural diffusion and enabling us to test our hypotheses using a sample of cultures with a diverse range of religious and social structures²⁶. The social structures of these cultures ranged from small kin-based groups to large, polities such as those found in Hawaii²⁷, meaning that that our sample is particularly well suited to testing hypotheses about the evolutionary transitions that occurred in early human civilizations²⁰. In the collection of ethnographic data, priority was given to primary ethnographic materials, collected by ethnographers nearest to the time focus. Each culture was coded by two trained coders and the ethnographic sources used for each culture, as well as the coding decisions, can be found in the Supplementary Information. The first coder found and reviewed suitable ethnographic materials and coded each of the variables. The second coder reviewed this decision based on a review of the sources consulted by the first coder and a search for any additional materials. The coders' decisions were highly consistent. In rare cases of disagreement, a third coder was consulted and a clear agreement was reached between all coders.

Tree building. To model the ancestral history of cultures we used a sample of 4,200 trees from the posterior distribution of a Bayesian analysis of Austronesian basic vocabulary items (the detailed method is described in Gray, Drummond, and Greenhill²⁵). The cultural history inferred by these language trees is corroborated by current genetic data³², and what is known from the archaeological record about the sequence and timing of cultural expansions²⁵. We pruned the original sample of 400 languages to 93, selecting those corresponding to cultures that were the subject of detailed ethnographic descriptions, while ensuring we sampled from all major cultural groupings and geographic regions.

Preliminary phylogenetic analyses. First, we used the multistate function in BayesTraits to test for patterns in the evolution of social stratification, without the influence of human sacrifice. While the discrete function in BayesTraits requires binary traits, the multistate function can be used to test how a trait with more than two states evolves²³. In this analysis we tested three different models of evolution. The first was unconstrained so that any transition between states could occur. For example, cultures could transition directly from being egalitarian to either moderate or high social stratification. The second model of evolution was constrained so that stratification must be gained in steps from egalitarian to moderately stratified, to highly stratified, but could be lost in jumps. For example, a culture could transition directly from being highly stratified to being egalitarian, but not vice versa. The third model of evolution was constrained so that social stratification must be gained and lost in sequential steps. This means that for a culture to go from being egalitarian to highly stratified, or highly stratified to egalitarian, it must pass

through a stage of being moderately stratified. We find that neither our second analyses that require cultures to gain social stratification in steps (BF = 0.08), or our third models that require the gain and loss of social stratification to occur in steps (BF = 1.28), were supported over the unrestricted models of evolution (Supplementary Tables 2–5). In the unconstrained analyses the mean transition rates between different states of social stratification were equal (Supplementary Table 2), and a range of different model were sampled in the posterior distribution (Supplementary Table 3). This suggests that cultures can transition freely between each different level of social stratification. These findings mean that in order to test how human sacrifice co-evolves with social stratification using BayesTraits, which requires binary traits, it is appropriate to group moderate and high stratification together as there could have been transitions directly to or egalitarianism from either form of stratification. These findings also mean that in order to test for the co-evolution of human sacrifice and high social stratification, it is appropriate to group egalitarianism with moderate social stratification as either could have transitioned directly to or from high social stratification.

We then tested for phylogenetic signal in our traits by using the *phylo.d* function in the R³³ package *Caper*³⁴ to calculate Fritz and Purvis' *D*³⁵, as well as whether this value differed significantly from what would be expected given no phylogenetic patterning, or under a Brownian model of evolution. We performed 1,000 permutations for each tree in our 4,200 tree sample, and we present the mean and standard deviation of these values across the sample of trees. A *D* statistic of 0 indicates that a trait is as phylogenetically conserved as would be expected under a Brownian model of trait evolution, while a value of 1 indicates that the distribution of the trait is not phylogenetically patterned³⁵. Our results indicate that human sacrifice is highly conserved ($D = -0.03$, s.d. = 0.09), and that its distribution is not significantly different from what would be expected under a Brownian model of trait evolution ($P = 0.54$), but is significantly different from what would be expected if there were no phylogenetic signal ($P < 0.01$). Our results also indicate that social stratification ($D = 0.19$, s.d. = 0.10) and high social stratification ($D = 0.18$, s.d. = 0.11) are phylogenetically patterned. The distribution of both social stratification and high social stratification was significantly different from that expected if there were no phylogenetic signal ($P = 0.01$ and $P < 0.01$, respectively), and not significantly different from that which would be expected under a Brownian model of evolution ($P = 0.39$ and $P = 0.38$, respectively). The strength of phylogenetic signal means that the assumptions of standard non-phylogenetic methods are violated, and that phylogenetic methods are appropriate to account for the historical dependencies between cultures^{36,37}.

Co-evolution models. Co-evolutionary analyses were performed in the phylogenetic software package BayesTraits²³. In order to inform our choice of priors for the MCMC analyses, we began by performing maximum likelihood (ML) analyses. Setting the number of optimisation attempts at 100 per tree, we calculated the mean transition rates for dependent and independent models across our sample of trees. For the models of human sacrifice and social stratification the mean transition rates ranged from 0.03 to 0.46. For the human sacrifice and high social stratification analyses the mean rates ranged from <0.01 to 0.39.

We then used the MCMC function in BayesTraits²³ to test for correlated evolution between traits. Using the MCMC function has the advantage of being able to test models of evolution across a sample of trees, rather than just one, which allows for phylogenetic uncertainty to be accounted for. We tested for co-evolution by comparing the likelihood of posterior distribution of dependent and independent analyses. Dependent analyses allow the evolution of one trait to depend on the state of another trait, and should be favoured when co-evolution has occurred. For example, the chance of a culture gaining high social stratification may be higher in cultures with human sacrifice than in cultures without. Independent analyses contain only models in which the evolution of one trait is independent of the other²³. For example, the chance of a culture gaining high social stratification will be the same for cultures with and without human sacrifice. In order to avoid over-parameterizing the model, we used a reverse-jump method that minimises the number of rate parameters used by only adding additional rate parameters when they improved the fit of the model. We used a hyper-prior seeding from an exponential distribution, and used the results of the ML analyses to inform the range of this hyper-prior. For all of our co-evolutionary analyses we set the hyper-before range from 0 to 0.5. Each analysis was run for 2×10^9 iterations, with the first 10^9 removed as a burn-in period. At the end of each run we calculated the log marginal likelihood by running a stepping-stone sampler³⁸ across the posterior distribution of the analyses. This stepping-stone sampler used a beta (0.40, 1.00) distribution and was run for 100,000 iterations across 1,000 stones. In order to ensure consistency we ran each analysis three times and reported the mean values across the run. As can be seen in the Supplementary Information, for all analyses, each of the three runs converged on highly consistent values (Supplementary Tables 6–16). We calculated Bayes Factors as twice the difference between the

log marginal likelihood of the posterior distributions of each analysis. Following Raftery³⁹ we take Bayes factors of 0–2 as providing no support for the models in one posterior distribution over the models in another posterior distribution, Bayes factors of 2–5 as providing positive support for one posterior distribution over the other, a Bayes factor of 5 to 10 as strong support, and a Bayes factor over 10 as very strong support.

To test why the dependent model was favoured over the independent model, we performed follow-up analyses in which the dependent model was constrained. By constraining the dependent model, we could force the MCMC chain to sample a subset of the models in the unconstrained dependent analyses. For example, to test whether human sacrifice affects the rate at which cultures gain high social stratification we forced the dependent analyses to sample only models of co-evolution in which cultures with and without human sacrifice have an equal chance of gaining high social stratification (rates b and d in Fig. 1e can be set to be equal). If human sacrifice were to affect the rate at which cultures gain high social stratification, then we should expect the constrained models to fit substantially more poorly than the unconstrained dependent models.

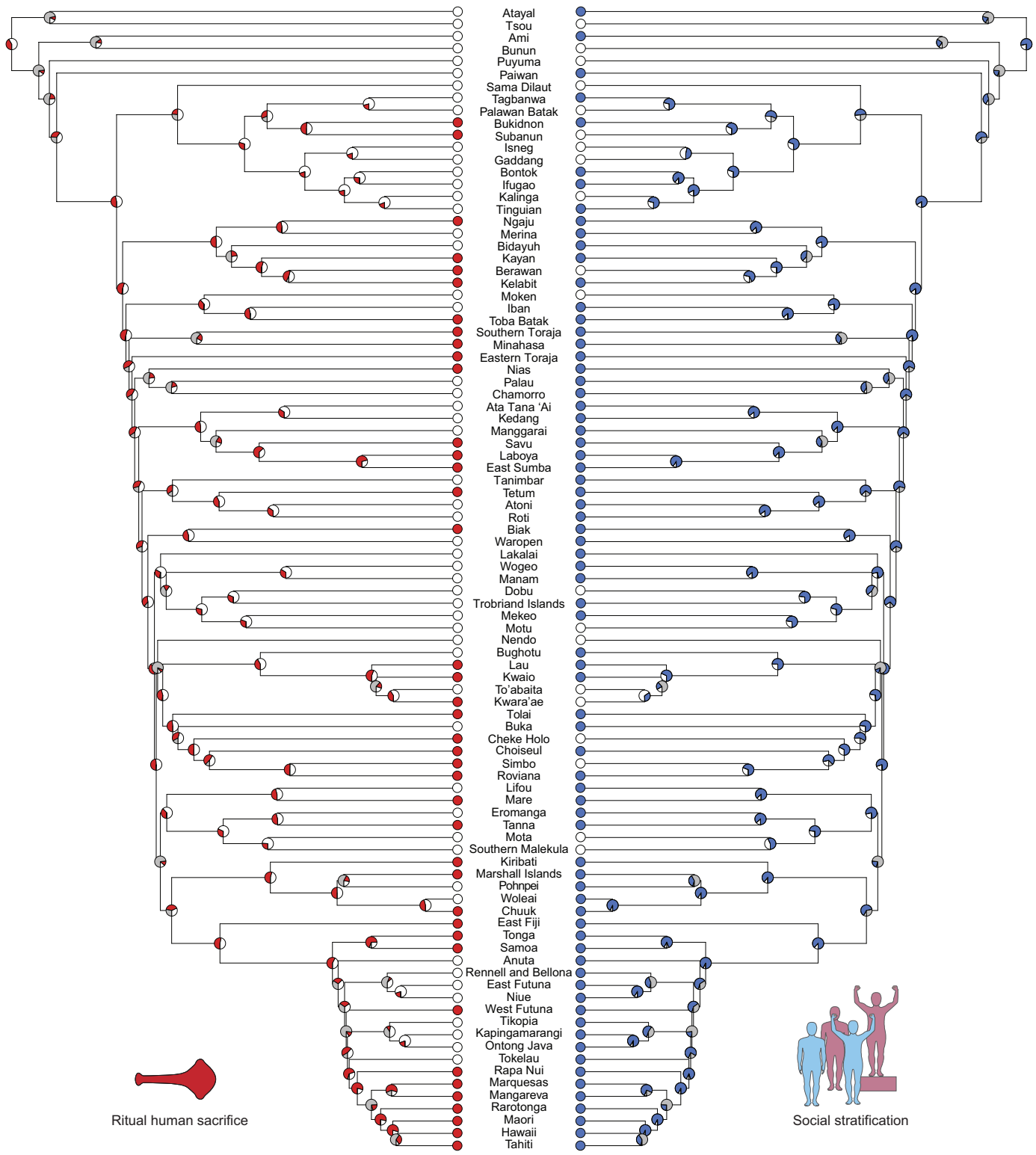
Validation of co-evolutionary models. In order to test for sampling effects we validated our co-evolutionary models by randomly sub-sampling 50% of cultures from the full analyses, and then re-ran all co-evolutionary models with this sub-sample. This process was repeated with 10 different random sub-samples (summarized in Supplementary Tables 17–26). Despite the reduced power of the smaller sample, we find support for the same pattern of evolution in the majority of random sub-samples. For the co-evolutionary analyses of social stratification and human sacrifice we find substantial or strong support for the models in the dependent analysis over the models in the independent analysis, as well the same pattern of co-evolution as that found in our full analyses, in eight out of ten random sub-samples. One of the remaining two sub-samples found substantial support for the same pattern of co-evolution, but no single model structure accounted for over half of those sampled in the posterior distribution and the most commonly sampled model structure differed from that of the full analyses. In the other remaining sub-sample, the dependent model suggested the same pattern of co-evolution but was not substantially supported over the independent model. For the co-evolutionary analyses of high social stratification and human sacrifice, we find strong or substantial support for the models in the dependent analyses over the models in the independent analyses, as well as the same pattern of co-evolution as that found in our full analyses, in seven out of the ten randomly selected sub-samples. In the three remaining sub-samples, the dependent model indicated the same pattern of co-evolution as in our full analyses, but the dependent models were not substantially supported over the independent models. The results of these random sub-sampling analyses indicate that our findings are robust across a wide range of randomly selected sub-samples and that even after substantially

reducing our power to detect correlated evolution we find support for the same relationship between social stratification and human sacrifice.

Recent simulation studies by Maddison and FitzJohn⁴⁰ have highlighted the potential for phylogenetic methods to lead to spurious correlations when one or more of the traits has undergone only a small number of evolutionary transitions such as one or two changes on a tree. As can be seen in Fig. 2 and Extended Fig. 1, both human sacrifice and social stratification are likely to have undergone a far greater number of changes than this, and these changes are distributed throughout Austronesia, indicating that the issues identified by Maddison and FitzJohn⁴⁰ do not apply to our study.

Figure construction. We created Fig. 2 and Extended Data Fig. 1 using a maximum clade credibility consensus tree from the full sample of trees using the software programme TreeAnnotator⁴¹. Trees were plotted using the `plot.phylo` function in the R package `ape`⁴², and the node values were plotted using the `nodelabels` function. The probabilities assigned to the nodes of the tree were calculated by using the `addnodes` function in `BayesTraits`²³, and represent the mean values assigned to nodes in the posterior distributions of the MCMC analyses. In these figures, grey was labelled 'phylogenetic uncertainty', and was used to illustrate the proportion of the trees in the sample for which that specific node of the consensus tree was absent.

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Extended Data Figure 1 | Phylogenetic distribution of human sacrifice and social stratification in Austronesia. Ancestral state reconstruction of human sacrifice and general social stratification on a maximum clade credibility consensus tree of 93 Austronesian languages. This analysis was run for 2×10^9 iterations and replicated three times. Pie charts at the

nodes represent the probable ancestral state inferred in an unconstrained dependent reversible-jump Markov chain Monte Carlo²³ analysis. Grey represents the proportion of our sample of 4,200 trees in which that node is absent.