

# Headhunting and Warfare in Austronesia: A Phylogenetic Comparative Analysis\*

Boris Gershman<sup>†</sup>                      Tinatin Mumladze<sup>‡</sup>  
American University                  American University

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## Abstract

Headhunting – the practice of acquiring human heads for ritual purposes – was historically widespread around the world. We hypothesize that headhunting represented a cultural response to frequent inter-tribal warfare and served as a mechanism to train warriors ready to defend their community. The practice was effective since, first, it allowed verification of warrior quality based on performance in headhunting raids and, second, it offered a system of rewards for men to develop and refine warfare skills. We use phylogenetic comparative methods and ethnographic data to empirically investigate this hypothesis in a sample of preindustrial Austronesian societies. Headhunting turns out to be substantially more prevalent in societies exposed to frequent warfare, accounting for shared cultural ancestry and a host of potentially confounding characteristics. Furthermore, Bayesian estimation of correlated evolution models suggests that, consistent with our hypothesis, the adoption of headhunting typically followed increases in warfare frequency and the decline of this practice was preceded by reduced intergroup conflict.

*Keywords:* Austronesia, Conflict, Correlated evolution, Culture, Headhunting, Phylogenetic comparative methods, Supernatural beliefs, Warfare

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<sup>†</sup>Corresponding author. Department of Economics, American University, 4400 Massachusetts Avenue NW, Washington, DC 20016-8029 (e-mail: boris.gershman@american.edu).

<sup>‡</sup>Department of Economics, American University, 4400 Massachusetts Avenue NW, Washington, DC 20016-8029 (e-mail: tm3538a@american.edu).

# 1 Introduction

The view of cultural beliefs and practices as environmental adaptations performing important functions, such as enforcement of cooperation, resource management, and community defense, has a long tradition in anthropology. More recently, economists also began to study the origins and historical determinants of culture by focusing on its social benefits, particularly in societies lacking modern technologies and formal institutions.<sup>1</sup> This paper adds to this burgeoning research agenda by investigating headhunting, the practice of acquiring human heads for ritual purposes. We hypothesize that headhunting represented a cultural response to frequent warfare and provide supporting empirical evidence from a sample of preindustrial Austronesian societies.

Although no longer in existence, headhunting was historically practiced around the world (Heron, 2020). We focus on Austronesia, a vast region in the Indo-Pacific where headhunting was fairly widespread prior to the early twentieth century, as documented in a rich ethnographic literature. Local practitioners believed that provision of human heads and their use in public ceremonies ensured plentiful harvests, prevented sickness, and generally secured material and spiritual well-being of their communities. For men, participation in successful headhunting raids was an important avenue for gaining social status, political power, and advantage in the marriage market.

Based on ethnographic evidence and theories of human trophy taking, we argue that headhunting served as an effective mechanism for training warriors providing community defense. The practice and surrounding beliefs offered substantial rewards to young men for developing warfare skills and engaging in risky missions. Their performance could be reliably verified by community members observing acquired heads, an ultimate proof of personal valor and success of the raid. Thus, headhunting addressed the notorious collective action problem in warfare by providing appropriate participation incentives and accurately rewarding skilled fighters. Since such a social arrangement is most valuable in communities facing severe external threats, we hypothesize that headhunting was more likely to be adopted and persist in societies exposed to frequent inter-tribal warfare.

We use the data from *Pulotu*, an ethnographic database of over a hundred preindustrial Austronesian societies (Watts et al., 2015a), and apply phylogenetic comparative methods to empirically investigate this hypothesis. Although not commonly used by economists, this set of techniques allows to account for cultural non-independence between societies due to shared ancestry and directly explore the coevolution of various cultural traits (Mace and

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<sup>1</sup>See Gershman (2017), Leeson (2017), and Lowes (2023) for an overview.

Pagel, 1994; Nunn, 2011). Our first set of results, based on phylogenetic logistic regression analysis, shows that there is a strong positive association between frequent warfare and the presence of headhunting, which holds after accounting for potentially confounding factors such as geographic and cultural isolation, social complexity, and subsistence production mode. In order to examine the likely causal directions in this relationship, we next estimate joint cultural dynamics of headhunting and frequent warfare within the correlated evolution framework (Pagel, 1994). Our results suggest that the adoption and decline of headhunting followed, respectively, the increase and reduction in warfare frequency. In contrast, the rate of change in warfare frequency was unrelated to the presence or absence of headhunting. These findings support our hypothesis that headhunting was a cultural adaptation to recurrent warfare.

This paper contributes primarily to two strands of literature. First, we expand the research agenda on the origins of culture within economics, particularly the study of traditional practices and beliefs that may at first seem unusual, harmful, or lacking a clear purpose or social benefit (Posner, 1980; Leeson, 2017). Some examples include reliance on ordeals in establishing guilt or innocence (Leeson, 2012; Leeson and Coyne, 2012; Maltsev, 2020), use of oracles in resolving interpersonal disputes (Leeson, 2014b), beliefs in the evil eye and witchcraft (Gershman, 2015; 2022). A common theme in these studies is that seemingly peculiar customs and supernatural beliefs serve important functions (e.g., administering justice, protecting property, and maintaining social order) in societies lacking alternative means of achieving those goals, such as effective government institutions or advanced technologies. Similarly, in our context, headhunting secures community protection in the absence of modern army structures and military equipment.

Within this literature, studies relating cultural arrangements to the challenges of collective defense and warfare are especially relevant to our work. Leeson (2014a) argues that the practice of human sacrifice protected communities from external predation. According to his theory, exchanging valuable property for humans that are subsequently sacrificed makes a community poorer and thus less attractive for outside plunderers. Nunn and Sanchez de la Sierra (2017) argue that a bulletproofing ritual, still performed in parts of the Democratic Republic of the Congo, mobilized community combatants to successfully repel external aggression. This ritual, ostensibly providing immunity against enemy bullets, caused individual combatants to underestimate the risk of fighting and induced greater combat effort on their part, which ultimately resulted in a higher level of community protection. Maltsev (2021) proposes that martyrdom, the idea that people gain spiritual benefits and status, often posthumously, for suffering as a result of fighting for

their religious beliefs, fostered rebellious collective action by lowering the private costs of participants in case of failure. In an argument closely related to our conceptual framework, Piano and Carson (2020) suggest that the practice of scalp-taking among Native Americans solved the problem of monitoring the performance of warriors on the battlefield. Importantly, these studies linking culture to warfare largely rely on qualitative evidence to support their respective theories. In contrast, we conduct a comprehensive empirical investigation directly addressing the issues of confounding factors and likely directions of causality in the relationship between headhunting and frequent warfare.

There is, of course, a vast literature on the social functions of cultural practices and beliefs outside economics. The most directly relevant part of this research explores the role of religion in fostering collective action and participation in warfare (Glowacki and Wrangham, 2013; Alcorta and Sosis, 2022). In a seminal paper, Sosis et al. (2007) show that, in a sample of 60 preindustrial societies around the world, the harshest male initiation rituals are observed in communities exposed to frequent intergroup warfare. The authors rely on costly signaling theory to argue that violent rites of passage promoted cohesion among men and created a standing class of warriors for protection. Johnson (2008) reviews various channels through which religious beliefs and practices support group cohesion and improve combat performance in intergroup conflict.

The second research agenda to which we contribute is the study of cultural evolution using phylogenetic comparative methods. Since the application of this approach requires linguistic trees, assumed to represent ancestral relationships between societies, most studies focus on ethnolinguistic clusters for which reliable phylogenies are available, such as the Austronesian, Bantu, and Indo-European families. Examples of cultural traits examined in this literature include kinship systems, marriage patterns, social hierarchies, and religious beliefs (Mace and Zhang, 2023). More narrowly, we contribute to the research on Austronesian cultures which so far explored such features as political complexity (Currie et al., 2010), marital residence patterns (Fortunato and Jordan, 2010), supernatural punishment (Watts et al., 2015b), human sacrifice (Watts et al., 2016), kinship terminology (Passmore and Jordan, 2020), games (Leisterer-Peoples et al., 2021), and gender-specific initiation rites (Bentley et al., 2021).

Although, to the best of our knowledge, phylogenetic comparative methods employed in our empirical analysis have not been previously used in economics, there is an active research agenda on the effects of ancestral relationships between populations on socioeconomic outcomes. For example, linguistic and genetic distances were used to measure cultural proximity and explore its implications for technological diffusion, migration deci-

sions, trade flows, and wars (Spolaore and Wacziarg, 2016; Ginsburgh and Weber, 2020). Linguistic distances have also been used to account for relatedness between groups when building indices of ethnolinguistic diversity (Gershman and Rivera, 2018). Statistical inference issues related to cultural non-independence of populations have been largely ignored in the relevant economics literature, apart from occasional attempts to account for it by clustering standard errors at the language family level or approximating the process of cultural diffusion via a phylogenetic version of the spatial lag model (Gershman, 2015). As illustrated through our examination of headhunting and warfare, phylogenetic comparative methods offer a powerful toolkit for directly incorporating and exploiting the structure of ancestral relationships between societies in cross-cultural statistical analyses.

The rest of this paper is organized as follows. Next section provides a primer on the practice of headhunting in Austronesia. Section 3 lays out a conceptual framework of headhunting as a cultural adaptation to frequent warfare. Section 4 introduces the data used in the analysis and describes preliminary patterns. Section 5 presents the main empirical results. Section 6 concludes. Appendices contain further information on the data and additional analyses.

## 2 Headhunting in Austronesia: A primer

*No! The custom is not horrible. It is an ancient custom, a good, beneficent custom, bequeathed to us by our fathers and our fathers' fathers; it brings us blessings, plentiful harvests, and keeps off sickness, and pains.*

Aban Avit, a Kayan chief, as quoted in Furness (1902)

Headhunting is the practice of acquiring human heads from outside communities that encompassed both the act of raiding and an array of surrounding rituals and beliefs. Hoskins (1996), among other scholars, emphasized the ritual meaning of headhunting to distinguish it from simple trophy taking and directly incorporated this notion in her widely-used definition of the practice as “an organized, coherent form of violence in which the severed head is given a specific ritual meaning and the act of headtaking is consecrated and commemorated in some form.” Similarly, Baldick (2013) stressed the importance of related beliefs and rituals when placing headhunting among the fundamental pillars of traditional Austronesian religions, and Simon (2012) argued that “without ritual, it is not headhunting, but rather merely a gruesome form of homicide.”

Headhunting was historically widespread across numerous islands of Southeast Asia and Oceania populated by Austronesian societies. Linguistic and phylogenetic compara-

tive analyses suggest that headhunting was likely practiced by the ancestors of all contemporary Austronesian peoples that inhabited the island of Taiwan over 5,000 years ago (Blust, 1995; Watts et al., 2015a). The first written records of headhunting among the Taiwanese aboriginal populations are found in Chinese sources dating back at least to the early 17th century (Baldick, 2013), but most of the ethnographic evidence was produced in the late 19th and early 20th centuries following active European contact with Austronesians. Throughout the past century, the practice was consistently suppressed by colonial administrations and centralized states across the region and it is now extinct, although some societies preserved headhunting-inspired rituals featuring coconuts, dolls, and other substitutes for human heads (George, 1996; Simon, 2012).

Despite some differences in the ways headhunting was performed in the region, cross-cultural comparisons reveal important similarities which provide a foundation for theorizing about the common purpose, or social function, of this practice. In what follows, we focus on these typical features of headhunting and also note some of the variations. We first briefly consider the two main aspects of the practice, that is, raid mechanics and associated rituals, and then turn to the key motives behind these seemingly puzzling behaviors.

Heads were usually taken during special headhunting raids, but sometimes as part of fighting motivated by other reasons (Downs, 1955). Some headhunting expeditions involved just a few men ambushing one or two victims, while others were performed by large groups attacking entire settlements, as observed among the Iban of Borneo and the Roviana of the Solomon islands (Aswani, 2000). While the number of heads was not essential for the ability to perform rituals, it did affect the status earned by individual headhunters and reflected the general success of the raid (Aswani, 2000; Watson Andaya, 2004). The attacks were typically aimed at out-groups, often neighboring tribes, although longer-distance travel could also be undertaken (McKinley, 1976; Schefold, 2007; Simon, 2012). More rarely, heads were collected from rival groups within the same larger society, like among the Ilongot of the northern Philippines (Rosaldo, 1980). The identity of victims varied from high-status individuals to anyone caught in an ambush, including women, children, and the elderly. Interestingly, the latter categories were sometimes considered a special prize demonstrating the headhunter’s ability to penetrate deep into foreign territory and capture “those very individuals whom men should protect” (Watson Andaya, 2004).

Headhunting raids, big or small, were not arbitrary and followed a well-defined protocol. Although the details of this protocol varied across societies and sometimes were very intricate, there is commonality to its basic structure involving the raid itself and activities preceding and following it (Baldick, 2013). Each headhunting party typically had a

leader, sometimes the tribal chief himself, who was responsible for organizing the raid and conducting preliminary rituals and investigations. Common pre-raid activities included selecting men suitable for the raid, consulting bird oracles and generally looking for good and bad omens in nature and dreams, asking gods for success in expedition and offering them animal sacrifices. Once the required rituals were completed, the raid was conducted on a day deemed favorable. Regardless of heads taken, an expedition was typically considered a failure if a group member was killed, in which case post-raid celebrations were limited or canceled. If a raid was carried out without losses, a choreographed community-wide celebration followed that could last for several days.

Upon their return, headhunters were greeted by other villagers, particularly women, who offered them congratulations, along with food and drink.<sup>2</sup> Further community activities included singing, dancing, feasting, recitation of myths, speeches praising the courage of headhunters, rites of passage for young men, sacrifices to the spirits of ancestors and local deities. Heads captured in the raid were usually placed on a pole and played an integral part in festivities. They were also “prepared” in advance by boiling, smoking, or temporary burying in the ground to remove flesh from the skull. In the process, bits of flesh and brain were sometimes eaten by headhunters ostensibly to acquire the vital force of their victims (Baldick, 2013). The skulls were then preserved within community and served as a sign of accumulated status (Aswani, 2000). Overall, although men obviously had the crucial role of procuring heads, headhunting was a “collective act with a divine nature” and engaged the entire community (Hung, 2020).

So, why did some Austronesian societies practice headhunting? A reasonable starting point is the list of reasons provided by the practitioners themselves. Numerous items on that list may be grouped into individual-level and collective-level motivations. Baldick (2013) summarizes both categories by stating that headhunting was performed to “obtain general prosperity and give the community strength and the headtaker prestige.”

Bringing heads was a universally accepted way for young men to display their fighting prowess, courage, and masculinity, qualities that made them desirable marriage partners (McWilliam, 1994; Simon, 2012). In some cases, headhunting success, marked by a special tattoo or dress, was actually required for marriage eligibility (Hoskins, 1996).<sup>3</sup> Headhunters acquired great status within their communities and could earn claims to political leadership

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<sup>2</sup>In some cases, like among the Toraja of Sulawesi, while headhunters were away, women engaged in a series of rituals and adhered to a variety of restrictions to ensure a successful raid (Downs, 1955).

<sup>3</sup>For example, in south-west New Guinea, community recognition of a marriage “was predicated on the husband’s participation in a successful raid, and a Jaqaj man was supposed to hang a head on the arm of his bride at the wedding feast” (Watson Andaya, 2004).

based on successful management of raids and the number of heads collected (McWilliam, 1996; Watson Andaya, 2004; Simon, 2012). Other, less frequently mentioned personal motivations vary from prosaic, such as getting released from debt, atoning for adultery, seeking revenge, or even simply venting emotions (Hoskins, 1996; Simon, 2012), to highly spiritual, such as earning a safe passage to afterlife (Hung, 2020).

In addition to these personal benefits earned by successful headhunters, the practice was widely believed to be essential for collective well-being, which commonly included such rewards as better agricultural crops, prevention of sickness and other misfortunes, and promotion of fertility among women (Hoskins, 1996; Schefold, 2007; Baldick, 2013). In some cases, these outcomes were presumably secured through gratification of deities to whom the captured heads were sacrificed. Besides these broad community-level benefits, severed heads were sometimes required to end periods of mourning and for mortuary rituals (Baldick, 2013). Occasionally they were also needed for inauguration of communal property such as longhouses and canoes (Dureau, 2000). Finally, pointing more directly to our hypothesis, some societies underscored the role of headhunting in defending their territory and resources against enemies (Watson Andaya, 2004; Simon, 2012).

The following basic patterns emerge from ethnographic accounts. First, both at the individual and collective levels, strong incentives were in place to motivate headhunting. Although participation was typically voluntary, young able men avoiding headhunting expeditions risked not getting married and effectively gave up their community status and prospects for political power. Second, communal-level benefits and rituals tied to headhunting clearly reflected the perceived crucial role of the practice for social welfare and the collective-good nature of successful raids. This was also manifested in the broad participation of community members in headhunting rituals and celebrations.

In the absence of quantitative data on the intensity of headhunting, ethnographic accounts provide qualitative evidence on such aspects as the frequency of raids, the fraction of men who participated in them, and the number of casualties. First, raids were conducted on a regular basis since heads were needed for systematically occurring events such as agricultural rites, consecration of communal property, and periods of mourning. At the same time, as pointed out by Geddes (1973) for the case of the Dayak people of Borneo, headhunting-related rituals were costly “in food and effort,” which limited the frequency of expeditions: there was “little temptation...to collect heads randomly or often.”

Second, participation of men in headhunting raids was relatively broad. Men with leadership ambitions and sometimes those simply wishing to be in a communally recognized marriage had to join a headhunting raid. Among the Toraja people, “all able-bodied



youths and men were eligible to participate and were expected to do so fairly frequently” (Downs, 1955). However, there were also numerous reasons for them to decline, including “fear, anger against one’s fellow villagers, the existence of a relative in the village to be attacked, ominous dreams or signs.” In other words, incentives and social pressure were in place to motivate broad-based participation in headhunting, while strictly speaking it remained voluntary and with a number of opt-out loopholes.

Third, based on the earlier description, headhunting raids were unlikely to have a high casualty rate among participants. They were carefully orchestrated, typically led by experienced headhunters, and designed to avoid unnecessary risk. Raids often represented ambushes targeting isolated individuals or small unprotected groups, and both the identity of victims and the quantity of obtained heads were not considered crucial for community rituals. On the other hand, a single headhunter’s death could render a raid a failure, which underscored the primacy of safe return. Simon (2012) notes how the rules and rituals associated with headhunting among the Sejiq people of Taiwan limited fatalities and frequency of expeditions. For example, the fact that all participants of a successful raid gained power and glory, and not just those who actually severed heads, “surely limited fatalities” and meant that relatively few raids could be sufficient for “all men in a small community to become eligible for facial tattoos.”

Interestingly, many features of Austronesian headhunting were also observed in societies far outside the region. For example, the reasons behind the practices of scalping and headhunting among Amerindian tribes, summarized in Chacon and Dye (2007), were strikingly similar to the ones listed above. At the individual level, these included desire for status, demonstration of fighting prowess, and securing a marriage. At the community level, like in Austronesia, human trophies were believed to enhance fertility among women, promote agricultural crops, appease local deities, and were sometimes required to end periods of mourning. High fertility and general prosperity were also the main motives behind headhunting among the Jivaro of South America, known for their “shrunk head” trophies, and the Naga of northeastern India (Baldick, 2013; Hoskins, 1996). Heron (2020) pinpoints some commonalities among twelve headhunting societies from around the world including status-seeking as a key factor driving participation in raids and the importance of community-wide ceremonies. The common features of headhunting and its presence in highly distinct societies suggest that the practice may have evolved independently multiple times and performed vital functions across communities.

### 3 Conceptual framework

Given the ethnographic evidence summarized above, we argue that exposure to frequent inter-tribal warfare, and the concomitant need for protection, were the fundamental factors in the adoption and persistence of headhunting. The building blocks of this argument were discussed in earlier studies on warfare and human trophy taking in small-scale preindustrial societies including, most recently, Johnson (2017), Heron (2020), and Piano and Carson (2020). Here, we bring these ideas together in Austronesian context and formulate the main hypotheses for our empirical analysis.

The survival of any society engaged in repeated intergroup conflict depends on its ability to maintain an effective class of warriors willing to tolerate risky and potentially deadly fighting. In the absence of centralized state, organized army, and modern technologies, creating proper incentives for taking such risk, even with the goal of providing an essential public good (community safety), is inherently complicated (Glowacki et al., 2020). The practice of headhunting represented a surprisingly comprehensive solution to this fundamental problem by addressing two key issues: 1) verification of warrior quality via accurate measurement of their performance in foreign territory and 2) provision of strong incentives for men to develop and practice required warfare skills.

The role of human trophies, heads in particular, as ultimate evidence of success in dominating the enemy has been universally accepted across societies, from Iron Age Europe and medieval Japan to pre-colonial Americas and Austronesia (Keeley, 1996; Aswani, 2000; Chacon and Dye, 2007; Heron, 2020). Unlike other trophies, such as limbs or personal belongings, a head is an incontrovertible proof of a single individual’s death. No person can remain alive without a head, and warriors cannot free ride by collecting multiple trophies from a single individual. Furthermore, a head sometimes makes it possible to verify the foreignness and status of the victim, providing further useful evidence to the community.<sup>4</sup> Taking a head is undoubtedly a costly signal of individual physical ability, skill, and courage since it requires not only killing the victim but also spending extra effort and incurring additional risk to sever the head and bring it back home (Johnson, 2017).<sup>5</sup> Thus, the practice of headhunting provided a unique mechanism for credibly measuring

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<sup>4</sup>McKinley (1976) argued that a head was the preferred trophy in Borneo partly because the face signified the “social personhood” of the enemy. The Amaya people of the Damer island also explained that, unlike bodies, heads were portable and clearly encoded “the identity of otherness” (Pannell, 1992).

<sup>5</sup>While the heads brought to camp sent this useful signal to in-group members, headless bodies in the foreign territory demonstrated military prowess and ferocity to the out-group.

warrior quality and success in environments where such evidence was difficult to obtain through other means.

In order for men to willingly participate in risky headhunting raids, they had to be properly rewarded. Hence, the second crucial element of the practice is a system of incentives and benefits available to headhunters. As discussed in the previous section, at the personal level, these came in the form of high social status and preferential treatment that comes with it, including best marriage opportunities and claims to political power. Even when enemy heads were not strictly required for marriage or formal transition to adulthood, men were also eager to participate in headhunting raids due to their perceived importance for the community as a whole. Since heads were believed to secure material and spiritual prosperity of the entire community, there was a clear understanding that warriors provided an essential public good and had to be rewarded for it.<sup>6</sup>

Furthermore, qualitative evidence indicates that headhunting was a carefully calibrated practice that was performed on a regular basis, encouraged broad-based participation, and had features limiting the number of casualties and frequency of raids. These properties made headhunting expeditions a suitable and relatively safe training ground for raising new warriors and maintaining their fighting skills.

In sum, the practice of headhunting provided an effective mechanism for securing combat-readiness in the face of intergroup conflict. Based on this, we hypothesize that headhunting was more socially valuable, and thus more prevalent, in communities exposed to frequent warfare. In addition, we argue that the adoption and demise of headhunting were dynamic cultural responses to changes in conflict frequency.

Existing evidence of such patterns is very limited. Heron (2020) explores twelve headhunting societies around the world, including several from Austronesia, and notes that all of them were characterized by a high level of intergroup violence. Similarly, in the context of scalping, Piano and Carson (2020) show that, across twelve North American cultural areas, the practice was largely present in regions with medium or high frequency of warfare. In the remainder of this paper, we use phylogenetic comparative methods to systematically investigate our hypotheses about the relationship between the presence of headhunting and warfare frequency in a large sample of Austronesian societies.

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<sup>6</sup>Both individual benefits reaped by headhunters and their perceived contribution to collective welfare may be seen as a special case of “cultural rewards” for participation in warfare in small-scale societies (Glowacki and Wrangham, 2013).

## 4 Data and preliminary patterns

### 4.1 *Pulotu* database and main variables

Our empirical analysis relies on *Pulotu*, an ethnographic database documenting historical and contemporary features of 137 Austronesian societies (Watts et al., 2015a; 2022). We focus on a subset of 129 societies for which data on headhunting and warfare are available. Both of these variables, along with other characteristics used in later analysis, belong to the “traditional state” section of the dataset capturing information prior to large-scale modernization. The majority of societies in our sample were pinpointed before the start of the 20th century, with 90% observed prior to 1935. Overall, *Pulotu* is comparable in nature to the *Ethnographic Atlas* and the *Standard Cross-Cultural Sample* datasets documenting preindustrial societies around the world and commonly used in quantitative social sciences (Lowes, 2021).

Headhunting, defined in *Pulotu* as a practice of killing people for the sole or primary purpose of obtaining their heads, is a binary variable (present or absent). Headhunting is found in 31% of societies in our sample and its distribution is mapped in figure 1. Warfare refers to lethal conflict with other societies and its frequency is coded on the following ordinal scale: frequent (18% of the sample), common (19%), occasional (26%), rare or never (37%). The rough frequency cutoffs separating these categories are one year, five years, and one generation. For a subset of our analyses requiring binary variables we create an indicator for frequent vs. infrequent warfare by grouping the first two and the last two categories of the original classification. Appendix B contains a map showing the spatial distribution of warfare frequency across societies in our sample.

Figure 2 shows the basic correlation between our variables of interest. Headhunting was only present in about 8% of societies that never or rarely engaged in lethal intergroup conflict. Its incidence rises sharply in societies with more frequent warfare, exceeding 50% in cases when it happened at least on a yearly basis. In terms of our binary warfare variable, headhunting was present in 50% (20%) of societies with frequent (infrequent) warfare.

This positive bivariate association is consistent with the view of headhunting as a cultural adaptation to frequent warfare. However, it does not necessarily imply the presence of a causal relationship of this kind for three reasons. First, this may be a spurious correlation driven by some omitted factors. Second, causality may also run in the opposite direction. Indeed, it is possible that headhunting raids generated response attacks trigger-

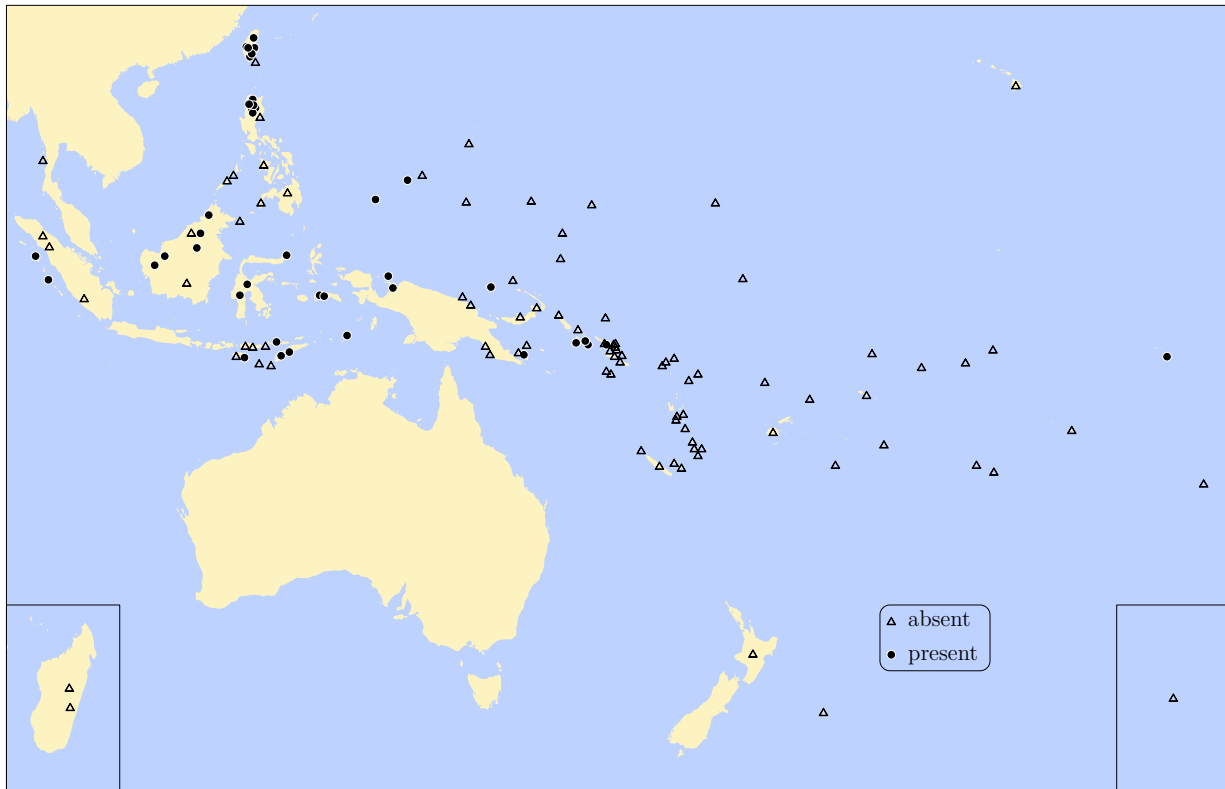


Figure 1: Spatial distribution of headhunting across Austronesian societies.

*Notes:* The inset maps in the bottom-left and bottom-right corners show Madagascar and Rapa Nui (Easter Island), respectively.

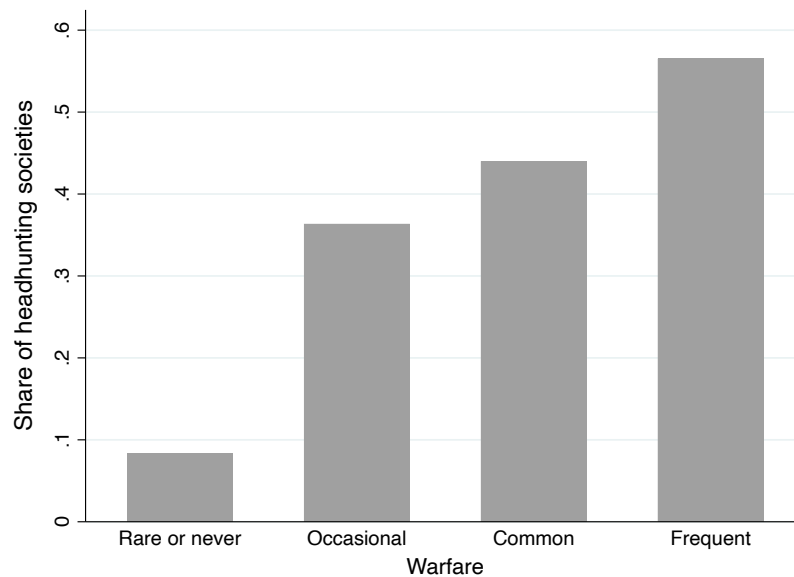


Figure 2: Correlation between warfare frequency and headhunting.

ing vicious cycles of revenge warfare and increasing its frequency.<sup>7</sup> Finally, a third problem for causal inference, pointed out by Francis Galton over a century ago but still commonly ignored in cross-cultural research, is the non-independence of observations in our sample due to shared ancestry. In other words, the observed correlation between headhunting and frequent warfare may simply reflect the process of cultural inheritance. Before addressing these three challenges through phylogenetic comparative methods, we set the stage for our analysis by matching *Pulotu* societies to respective Austronesian languages and formally investigating the presence of cultural non-independence in our sample.

## 4.2 Accounting for shared ancestry

In order to account for relatedness between species in statistical analyses of their traits, evolutionary biologists rely on phylogenetic trees inferred from molecular data. Drawing on parallels between biological and cultural evolution, anthropologists suggested that relatedness between societies, particularly ethnic groups, for the purpose of cross-cultural analyses can be approximated using linguistic trees inferred from language characteristics (Mace and Holden, 2005; Nunn, 2011). Once each society is linked to its language, phylogenetic comparative methods can subsequently be applied.

We follow this approach and match societies in our sample to Austronesian languages arrayed on time-calibrated linguistic trees by Gray et al. (2009). More specifically, the authors provide a sample of 4,200 trees from the posterior distribution of a Bayesian analysis of terms from the Austronesian Basic Vocabulary Database (Greenhill et al., 2008). This variety of likely linguistic trees reflects the problem of phylogenetic uncertainty, with each tree representing just one estimate of ancestral relationships between languages. As shown below, phylogenetic uncertainty can sometimes be directly incorporated in statistical analyses, while in other cases, we can test for robustness across the entire sample of trees or rely on a single “consensus” tree. Due to data limitations, we were only able to match 107 of 129 societies to Austronesian languages covered by Gray et al. (2009). We then pruned the trees accordingly, that is, eliminated languages outside of our sample while preserving the tree structure.

The joint distribution of binary headhunting and warfare frequency variables across societies placed at the tips of a consensus linguistic tree is shown in figure 3. Here, for the

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<sup>7</sup>The extent to which this mechanism is operational has been debated in the literature. For example, Heron (2020) argues that headhunting and warfare likely reinforced each other, while Johnson (2017) suggests that, by signaling their ability to inflict extra-lethal violence on their victims, headhunting societies could avoid a conflict spiral through deterrence.

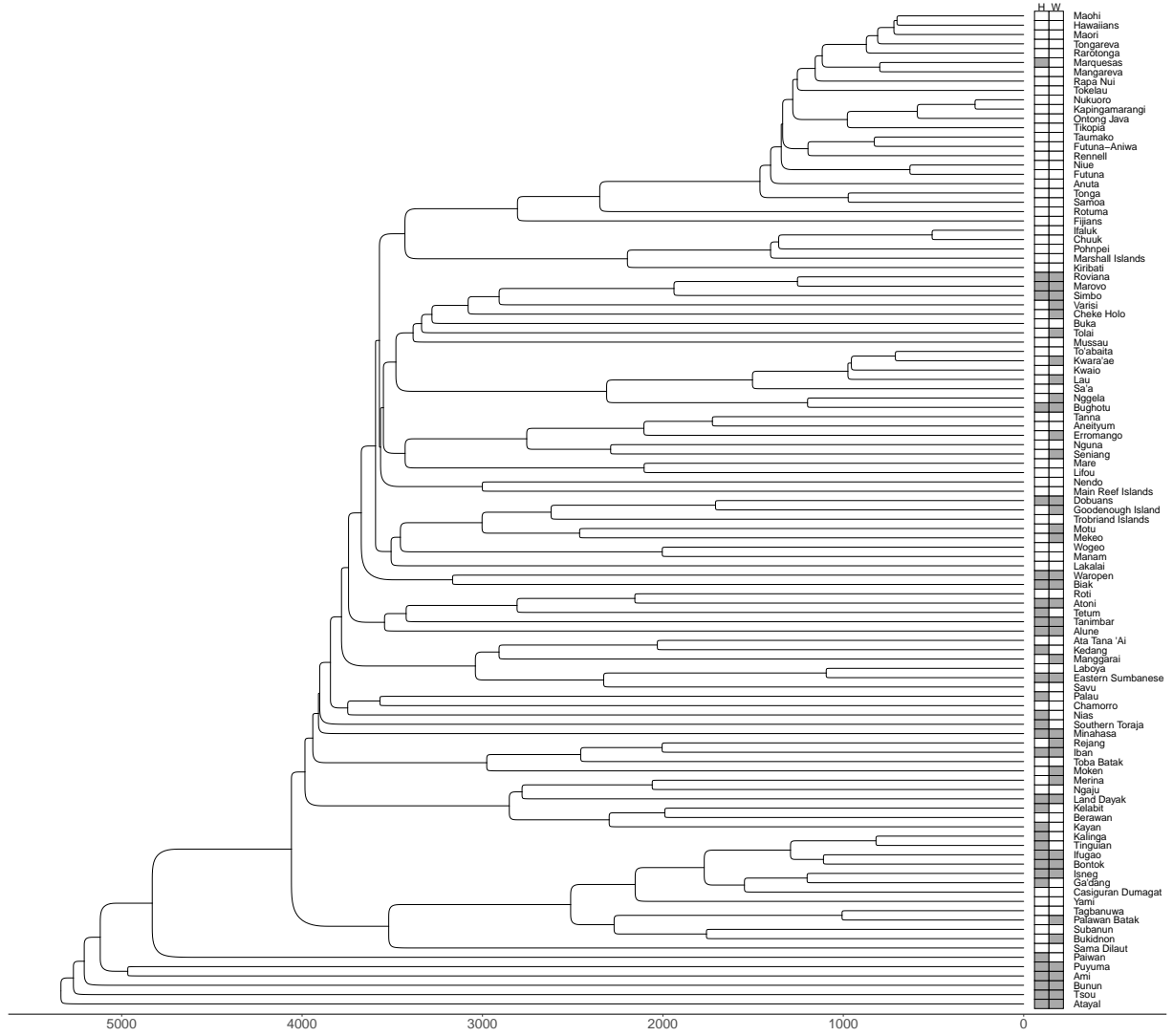


Figure 3: Headhunting and warfare at the tips of the linguistic tree.

*Notes:* Names of societies from our sample are listed at the tips of the maximum clade credibility tree of Austronesian languages. Shaded cells indicate the presence of headhunting (H) and frequent warfare (W) in respective societies. Horizontal axis represents time measured in years before present.

purpose of illustration, we use the so-called maximum clade credibility tree, a summary tree representing a “point estimate” based on the entire sample of 4,200 candidates (Heled and Bouckaert, 2013). The horizontal axis reflects time before present and the length of tree branches is measured in years. The root of the tree is placed at about 5,200 years ago, when the ancestors of all Austronesian populations began spreading from Taiwan throughout the Indo-Pacific region in a “pulse-pause” type of movement (Gray et al., 2009). Societies at the very bottom of the figure are the aboriginal settlers of Taiwan, whereas the large,

relatively recent clade at the top corresponds to Polynesia. A casual glance at the figure suggests that the observed trait values may not be randomly distributed with respect to the structure of the linguistic tree. For example, Polynesian societies typically lack both headhunting and frequent warfare, pointing to the possibility of shared cultural inheritance.

To formally investigate this issue, we tested both variables for the presence of phylogenetic signal using the  $D$  statistic specifically designed for the case of binary traits (Fritz and Purvis, 2010). A  $D$  statistic of 1 indicates that the trait is distributed independently of the tree structure (there is no phylogenetic signal), and a value of 0 corresponds to phylogenetic patterning implied by the Brownian motion threshold model of evolution. Negative values of  $D$  indicate that a trait is more phylogenetically conserved compared to the Brownian motion baseline. We computed the  $D$  statistic for each of the 4,200 trees, allowing 1,000 permutations per tree, and tested hypotheses corresponding to the reference cases of  $D = 0$  and  $D = 1$ . The resulting set of  $D$  statistics (with an average of  $-0.39$  and a standard deviation of  $0.09$ ) and formal tests imply that the headhunting trait contains a phylogenetic signal ( $p$ -values range between  $0$  and  $0.001$ ) and its observed distribution is not significantly different from what is expected under the Brownian motion model ( $0.39 < p < 0.93$ ). We get similar results for warfare frequency, with the average  $D$  statistic of  $-0.18$  (standard deviation of  $0.08$ ). Like headhunting, this trait has a strong phylogenetic signal ( $0 < p < 0.002$ ) and its patterning is consistent with the Brownian motion baseline ( $0.20 < p < 0.83$ ).

In sum, both traits at the center of our investigation are phylogenetically structured, likely reflecting cultural non-independence of Austronesian societies. As briefly mentioned earlier and is further illustrated in appendix C, failure to account for this non-independence between observations may lead to incorrect inference when standard statistical methods are applied. In contrast, phylogenetic comparative methods directly incorporate the information on cultural non-independence, contained in linguistic trees, in statistical models. This approach provides more accurate inference about the strength of association between traits and enables an analysis of likely causal directions in their relationship.

### 4.3 Comparing spatial and linguistic proximity

Although the problem of cultural dependence has been largely ignored by economists, the possibility of spatial dependence between observations received substantial attention (Conley, 2010). The standard assumption in spatial econometric methods is that geographic proximity between units of observation reflects their degree of interdependence. Perhaps the most commonly used method of accounting for spatial correlation in appli-



cations is the adjustment of standard errors following the approach of Conley (1999). It assumes a generalized structure of the covariance matrix of regression error terms and offers its estimator that weighs pairs of observations based on their spatial proximity. Note that this method does not assume any particular model of spatial propagation and leaves the coefficient estimates unchanged.

Unlike the Conley correction and other commonly used tools of spatial econometrics, phylogenetic comparative methods typically rely on explicit models of trait evolution on phylogenies to derive relevant estimators of both model parameters and their standard errors. In addition, some phylogenetic comparative methods go beyond simply “accounting” for cultural non-independence and exploit the structure of ancestral relationships between societies to model coevolution of traits over time, as illustrated in section 5.2. Finally, although spatial and phylogenetic dependence are conceptually related, below we show that geographic and linguistic proximity are substantively different metrics.

A standard measure of distance between two languages in our context is the estimated amount of time since divergence from their most recent common ancestor. In other words, it is the amount of time that those languages evolved independently of each other. It can be easily calculated based on a time-calibrated linguistic tree, such as the one shown in figure 3. Under special conditions, linguistic and geographic distances between cultures may be tightly correlated. However, the processes through which new ethnic groups and their languages emerge and evolve, including actual paths of geographic dispersal and subsequent migrations, are typically complex and result in relative locations of societies that are not necessarily aligned with their linguistic proximity. The process of Austronesian dispersal involved colonization of numerous islands throughout a vast region and proceeded in a sequence of expansion pulses and settlement pauses over thousands of years (Gray et al., 2009). The timing of those pulses and pauses was determined by many factors including available seafaring technologies, knowledge of navigation, geographic obstacles, and wind patterns. As a result, although the diversification of Austronesian languages was coupled with geographic expansions, “naive” measures of spatial proximity between societies often do not reflect the degree of their shared ancestry.

To illustrate such “mismatches” between spatial and linguistic distances, figure 4 combines a portion of the maximum clade credibility tree of Austronesian languages with a regional map pinpointing geographic locations of selected societies. First, consider three neighboring societies at the very top of the figure: Atayal and Puyuma of Taiwan and Yami of the nearby Orchid island. Pairwise geographic distances between these societies are relatively modest and do not exceed 270 kilometers. Yet, as can be seen from their po-

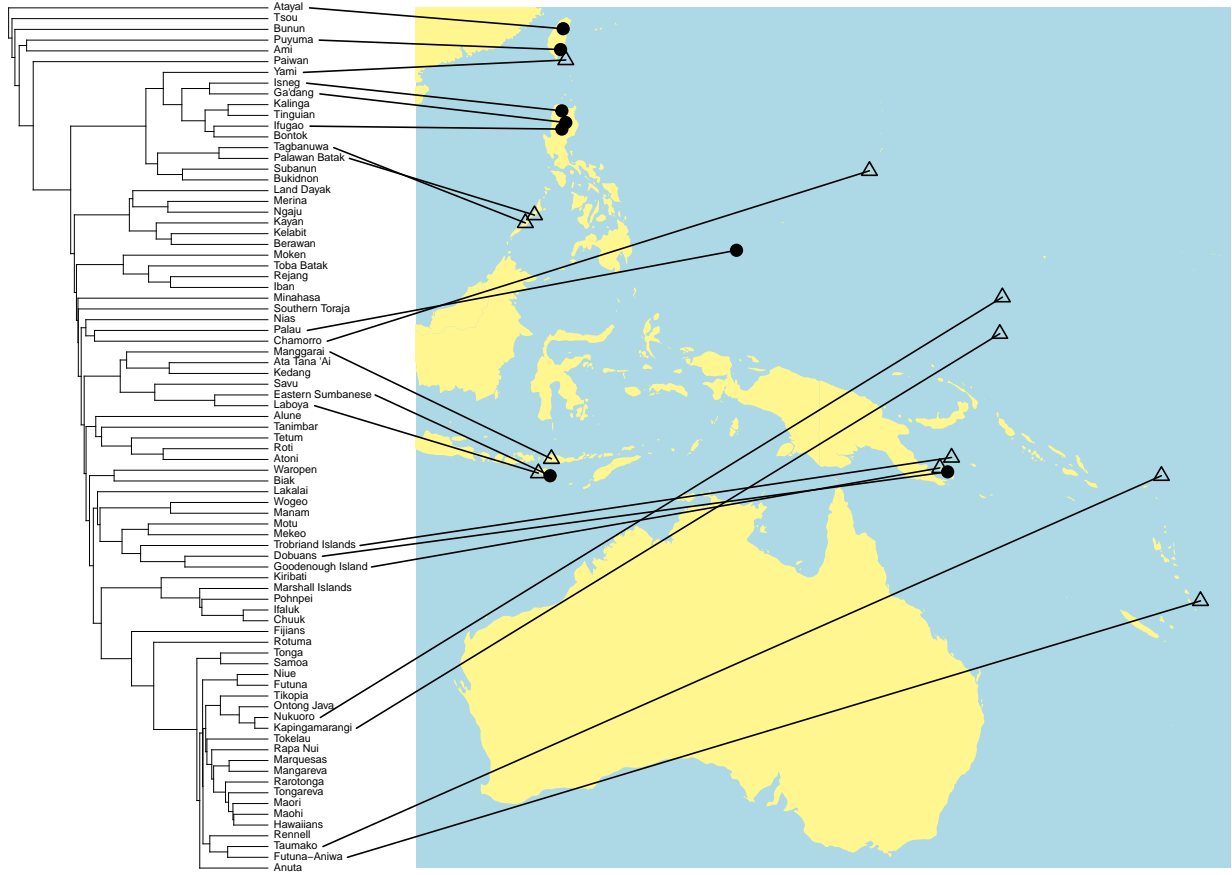


Figure 4: Spatial and linguistic proximity in a subsample of cultures.

*Notes:* The left-hand side of the figure shows a portion of the maximum clade credibility tree of Austronesian languages for 81 societies. As in figure 1, solid circles represent the presence of headhunting and hollow triangles mark its absence.

sitions on the linguistic tree, they are distant relatives whose ancestral languages diverged more than 5,000 years ago.

Next, consider another group of three neighboring societies in the middle of the figure: Laboya and Eastern Sumbanese of Sumba island and Manggarai of Flores. Again, all three are in close geographic proximity, within 170 kilometers of each other, but pairwise linguistic distances show a different pattern. Laboya and Eastern Sumbanese speak sister languages that diverged about a thousand years ago. However, both of them are linguistically much further away from the Manggarai, sharing the most recent common ancestral language more than 3,000 years ago. Thus, similar geographic distances in this case correspond to very different pairs of linguistic distances. Likewise, linguistic proximity does not necessarily imply spatial proximity, as can be seen from the case of Taumako (Solomon islands) and Futuna-Aniwa (Vanuatu) languages displayed at the bottom of the

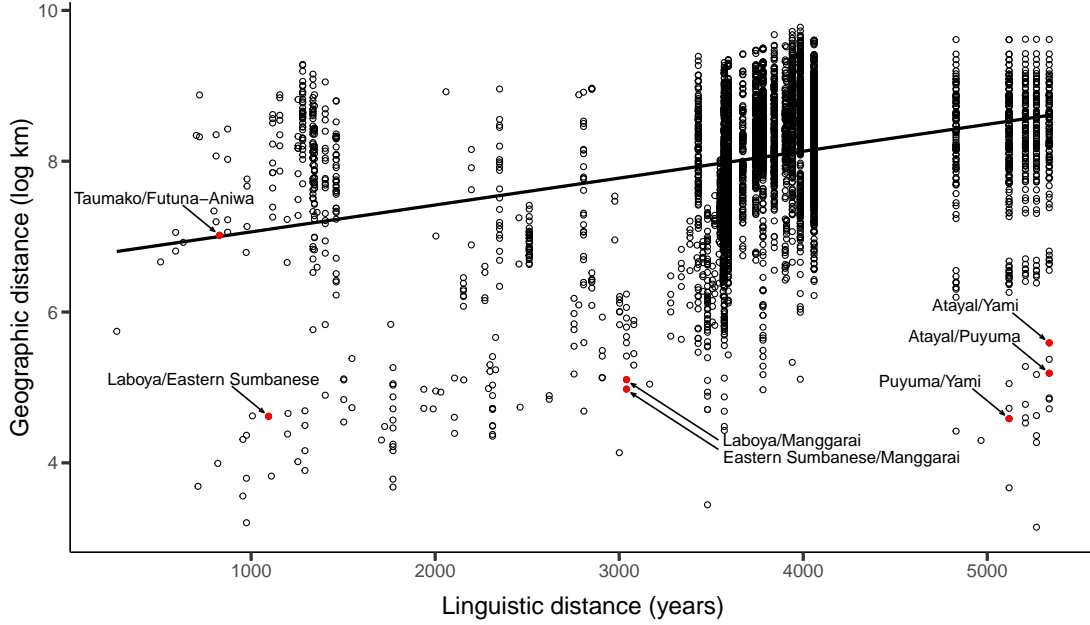


Figure 5: Relationship between pairwise geographic and linguistic distances.

*Notes:* Pairwise distances are computed for the full sample of 107 observations yielding 5,671 pairs. Geographic distance is the log-transformed great-circle distance in kilometers. Linguistic distance is the time since divergence from the most recent common ancestor computed based on the maximum clade credibility tree. Regression line is shown for the full sample of distance pairs. Solid points with arrows correspond to seven society pairs discussed in the text.

figure. Although they separated only some 800 years ago, the island locations of respective societies are more than 1,000 kilometers away from each other.

A scatterplot of all pairwise distances in figure 5 shows how the two measures compare across our entire sample. Geographic (great-circle) distances, ranging from about 25 to over 17,000 kilometers are log-transformed. Although spatial and linguistic distances are positively correlated, their correspondence is far from perfect.<sup>8</sup> Indeed, as can be seen from characteristic “columns” of data points in the figure, for many pairs with identical values of linguistic distance, there is a large variation in respective geographic distances.

In sum, standard ways of accounting for spatial correlation based on plain measures of geographic distance cannot fully capture the degree of shared ancestry as reflected in linguistic distances.

<sup>8</sup>The correlation coefficient is equal to 0.3 for log-transformed and 0.23 for raw geographic distances.

## 5 Phylogenetic comparative analysis

### 5.1 Phylogenetic regression approach

As mentioned earlier, a positive relationship between warfare frequency and the presence of headhunting is consistent with our main hypothesis, but it may also be driven by confounding factors. In this section, we examine this possibility in a phylogenetic regression setting that also accounts for cultural relatedness between observations in our sample.

Since our outcome variable, the presence of headhunting, is binary, we use the phylogenetic logistic regression model developed by Ives and Garland (2010). This is a generalization of the standard logit model, in which observations are phylogenetically structured. As in regular logit, the probability of an outcome variable  $Y$  taking the value of 1 is linked to a vector of regressors  $\mathbf{x}$  via a logistic function,  $\mathbf{P}(Y = 1|\mathbf{x}) = e^{\mathbf{x}\boldsymbol{\beta}}/(1 + e^{\mathbf{x}\boldsymbol{\beta}})$ , but the variance-covariance matrix of  $Y$  has a more complicated structure relative to the case of independent observations.

Specifically, the covariance elements of this matrix depend both on the strength of phylogenetic signal in the outcome variable, capturing the shared cultural evolutionary history of societies, and on the model’s regressors. The functional form of this covariance matrix reflects a two-step process assumed for the evolution of the binary trait  $Y$ . In the first step,  $Y$  evolves along the branches of a given phylogenetic tree according to a two-state continuous-time Markov process, with constant instantaneous probabilities of switching between 0 and 1 (Pagel, 1994). The sum of these probabilities, or the overall transition rate  $\alpha$ , measures the strength of phylogenetic signal in trait  $Y$ , with greater values (higher switching rates) corresponding to weaker signal. This process gives rise to a probability distribution for trait values at the tips of the phylogenetic tree. In the second step, following the evolution of  $Y$  along the tree branches, its values are further affected by regressors in a way that no longer depends on phylogeny. Thus, the first step of the evolutionary process determines the correlation of trait values between societies, whereas its second step sets the mean trait values in response to independent variables.<sup>9</sup> Note that the estimated value of  $\alpha$  in this setting only reflects “residual” phylogenetic signal in  $Y$  unexplained by regressors.

In the absence of phylogenetic signal, that is, when  $\alpha$  approaches infinity, this model collapses to the standard logit framework. However, when the signal is present, standard logit estimates are biased and subject to inflated type-I errors (Ives and Garland, 2010).

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<sup>9</sup>See Ives and Garland (2010) and Ho and Ané (2014) for technical details of the model and the exact structure of the covariance matrix for  $Y$ .

We estimate the phylogenetic logistic regression model using the algorithm proposed by Ho and Ané (2014) and implemented in the `phylolm` package for R software. This algorithm is linear in the number of tips of the phylogenetic tree and allows fast estimation of regression coefficients  $\beta$  and phylogenetic signal  $\alpha$  based on a quasi-maximum-likelihood approach. We use the maximum clade credibility tree in the baseline analysis and show in appendix E that our results are robust across the entire sample of linguistic trees from Gray et al. (2009).

We control for a range of characteristics that could confound the relationship of interest by affecting the presence of headhunting, frequency of warfare, or both, as suggested by earlier work on culture and conflict.<sup>10</sup> Our first group of control variables includes the approximate year observation for each society and two measures of isolation. These are geographic remoteness, namely, the (log-transformed) distance to the closest landmass inhabited by a different society, and cultural assimilation, as captured by the presence of influence from major world religions (Christianity, Islam, Buddhism, or Hinduism) on local supernatural beliefs. Altogether, these variables to some extent account for spatial barriers to cultural diffusion of headhunting and its possible decline as a result of exposure to foreign religious traditions and prolonged contact with outside cultures and colonial administrations. The same measures, particularly geographic isolation, could simultaneously affect the incidence of warfare (Younger, 2008).

Second, we control for several metrics of social complexity: (log) population size, level of political authority, and social stratification. Population size has been argued to be an important determinant of general cultural complexity, warfare, and the pace of religious conversion in small-scale societies (Fogarty and Creanza, 2017; Younger, 2008; Watts et al., 2018). The presence and type of political authority and degree of social stratification have both been linked to headhunting in previous studies. Simon (2012) argues that headhunting was in part an attempt by ambitious men to augment their political power, which could in principle lead to the development of incipient chiefdoms. Similarly, Aswani (2000) views headhunting as a means to validate political and spiritual authority by the Roviana chiefs.<sup>11</sup> Heron (2020) hypothesizes that headhunting was more likely to emerge in societies that

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<sup>10</sup>Detailed definitions and summary statistics for all variables are reported in appendix A.

<sup>11</sup>The role of violence in gaining prestige and accumulating or asserting political power has been observed throughout human history (Gat, 2008). In small-scale societies, it frequently had ritualistic components which may appear particularly gruesome, as in the cases of headhunting or human sacrifice. In many larger-scale societies, such as the ancient Rome, political advancement was often based on successful military campaigns (Harris, 1985) that arguably resulted in a far greater number of victims than the ritualized violence of headhunting tribes.

were relatively egalitarian, but allowed for some degree of authority and leadership. Both interpersonal and intergroup violence have also been associated with the extent of social and political hierarchy in societies (Gat, 2008).

Finally, we account for differences in subsistence production mode through two binary variables. One captures agriculture or horticulture as predominant sources of food and the other indicates land-based group hunting as a non-negligible subsistence activity. As mentioned in section 2, headhunting was often believed to be essential for securing good crops, providing a possible link to reliance on agriculture for subsistence. On the other hand, some studies suggest that human trophy taking may have derived from group hunting of animals (Piano and Carson, 2020), which motivates the inclusion of our second variable. The type of subsistence production mode may also have indirect effects on the variables of interest through the degree of inequality and social complexity (Gershman, 2015).

Table 1 presents estimation results for different specifications, with data availability dictating respective sample sizes. The coefficients corresponding to warfare frequency are positive and statistically significant across the board, even in the most demanding specifications.<sup>12</sup> Table 2 reports the relevant average marginal effects, along with the 95% bootstrap confidence intervals. These estimates are large and imply that, other things equal, societies with occasional or common inter-tribal warfare are about 20-35 percentage points more likely to practice headhunting relative to those in which warfare is rare or non-existent. The average increase in that likelihood associated with frequent warfare exceeds 50 percentage points.

Among other covariates, the influence from major religions enters with a negative sign and is statistically significant in 3 out of 5 specifications, suggesting that contact with outside cultures is negatively associated with the presence of headhunting. In specifications of columns 5–8, geographic remoteness also enters with a negative sign and is statistically significant in two specifications, consistent with the absence of headhunting in more isolated cultures. Importantly, larger societies and those with political authority present at local or supralocal levels are more likely to practice headhunting, in line with the arguments mentioned earlier. On the other hand, social stratification and production mode indicators are not statistically significant.

Regression results show that the positive relationship between warfare frequency and headhunting is not driven by other relevant characteristics and is robust to accounting

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<sup>12</sup>Following the recommendations of Ives and Garland (2010; 2014), we also calculated bootstrap confidence intervals for all coefficient estimates, without qualitative changes in statistical significance.

Table 1: Phylogenetic logistic regression estimates

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
<b>Warfare</b>								
Occasional	1.898** (0.871)	2.158** (0.879)	1.807** (0.778)	1.608** (0.765)	2.276*** (0.742)	2.051*** (0.746)	1.813*** (0.696)	1.995*** (0.748)
Common	2.122** (0.888)	2.700*** (0.936)	2.284*** (0.818)	1.977** (0.792)	2.102*** (0.780)	2.216*** (0.772)	1.688** (0.770)	2.204*** (0.851)
Frequent	3.406*** (1.080)	3.681*** (1.072)	3.286*** (0.996)	3.422*** (1.050)	2.713*** (0.900)	2.963*** (0.957)	2.548*** (0.913)	3.351*** (1.094)
<b>Year of observation</b>		0.695 (0.620)	0.297 (0.539)	0.086 (0.551)	0.218 (0.626)	0.115 (0.644)	0.217 (0.631)	−0.002 (0.648)
<b>Geographic isolation</b>			0.013 (0.135)	0.014 (0.130)	−0.285* (0.169)	−0.446** (0.189)	−0.209 (0.169)	−0.288 (0.200)
<b>Major religion</b>				−0.716 (0.596)	−1.584** (0.789)	−2.593*** (0.964)	−0.888 (0.711)	−2.475** (0.998)
<b>Population size</b>					0.451** (0.192)	0.432** (0.194)	0.267 (0.200)	0.346* (0.204)
<b>Political authority</b>								
Sublocal						0.087 (1.288)		0.839 (1.385)
Local						1.483* (0.886)		1.845* (1.035)
Supralocal						1.573* (0.942)		1.889* (1.065)
<b>Social stratification</b>								
Moderate							0.182 (0.680)	
High							0.147 (0.832)	
<b>Agriculture</b>								1.001 (0.720)
<b>Group hunting</b>								0.733 (0.696)
Phylogenetic signal $\alpha$	0.13	0.13	0.12	0.08	0.20	0.20	0.27	0.19
Observations	107	107	107	102	96	92	85	88

Notes. Dependent variable is the presence of headhunting. Omitted categories are: “rare or never” for warfare, “absent” for political authority and social stratification. \*\*\*, \*\*, and \* denote statistical significance at the 1, 5, and 10 percent level, respectively.

for cultural non-independence between observations.<sup>13</sup> However, they do not rule out the possibility of reverse causality. A standard approach to estimating the causal effect of interest would rely on identifying a source of exogenous cross-sectional variation in warfare frequency and pursuing an instrumental variables strategy. Finding such quasi-random variation is notoriously challenging. Instead, in the next section, we follow an alternative

Table 2: Average marginal effects for warfare frequency

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Occasional	0.183 (-0.12, 0.64)	0.220 (0.07, 0.49)	0.207 (0.01, 0.53)	0.175 (-0.01, 0.53)	0.378 (0.18, 0.54)	0.335 (0.10, 0.50)	0.352 (0.12, 0.53)	0.324 (0.08, 0.48)
Common	0.224 (0.00, 0.64)	0.334 (0.17, 0.59)	0.308 (0.13, 0.59)	0.246 (0.04, 0.60)	0.342 (0.13, 0.54)	0.367 (0.13, 0.54)	0.324 (0.07, 0.54)	0.364 (0.09, 0.54)
Frequent	0.525 (0.22, 0.78)	0.567 (0.38, 0.75)	0.552 (0.29, 0.75)	0.584 (0.29, 0.77)	0.466 (0.21, 0.66)	0.505 (0.21, 0.66)	0.508 (0.19, 0.69)	0.562 (0.24, 0.67)
Observations	107	107	107	102	96	92	85	88

*Notes.* Omitted category is “rare or never.” For each estimate, 95% bootstrap confidence intervals are provided (based on 10,000 replications).

approach to directly explore the coevolution of headhunting and warfare frequency in a framework that suggests the likely causal directions in this relationship. The key insight at the core of this approach is that a representation of our cross-sectional data on a linguistic tree uncovers an implicit time dimension: the current distribution of traits is the outcome of their temporal coevolution over the course of Austronesian expansion. This insight allows to set up a model of joint dynamics of headhunting and warfare frequency along the branches of a linguistic tree. In this evolutionary model of descent with modification, each trait may randomly change its value at any moment in time and the probability of such change may depend on the value of the other trait. By estimating the rates of change and testing relevant restrictions on these rates, we can infer the likely order of trait evolution over time providing suggestive evidence on the directions of causality.

## 5.2 Correlated evolution framework

### 5.2.1 Model setup and estimation approach

We employ the model of correlated evolution of binary traits on phylogenies developed by Pagel (1994) and adapted in subsequent research to examine cultural dynamics. In our application, the traits are headhunting and frequent warfare, and their observed bundles across Austronesian societies are represented in figure 3. Since each trait can only take the values of 1 (present) and 0 (absent), there are four possible combinations of trait values, or states.

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<sup>13</sup>Estimates of  $\alpha$  at the bottom of table 1 show a moderate phylogenetic signal, which validates our use of the phylogenetic logistic regression model. Note that these values are technically not comparable across specifications due to differences in samples (and thus, linguistic trees employed in the estimation). Appendix D presents standard logit estimates for reference.



Each trait is assumed to evolve along the phylogenetic tree according to a continuous-time Markov process.<sup>14</sup> The probability of change in trait value depends only on the initial state at the beginning of the relevant tree branch, but not on previous history. Instantaneous transition rates between values 0 and 1 are assumed to be constant, and the possibility of both traits changing their values in the same instant is ruled out (this, however, can happen over a longer period of time).

Given these assumptions, there are eight transition rates, denoted as  $q_{ij}$ , connecting different states. The subscripts  $i$  and  $j$  identify the initial and final states of a particular transition, respectively, and their possible values 1, 2, 3, and 4 correspond to states (0, 0), (0, 1), (1, 0), and (1, 1), as illustrated in figure 6. For example, in our analysis,  $q_{24}$  captures the probability of acquiring the practice of headhunting over an infinitesimally short time interval from the state in which warfare is frequent, but headhunting is absent.

If traits evolve independently, the rates of change in the values of one trait do not depend on the value of the other trait. In such a model of independent evolution,  $q_{12} = q_{34}$ ,  $q_{13} = q_{24}$ ,  $q_{21} = q_{43}$ , and  $q_{31} = q_{42}$ , that is, there are at most 4 distinct parameters to estimate. By testing the above constraints, one can distinguish between independent and correlated evolution of traits. In addition, as shown below, specific constraints on transition rates can be tested to examine the order of trait evolution.

In his original paper, Pagel (1994) showed how to find maximum likelihood (ML) point estimates of transitions rates, given the observed data and phylogeny, and test constraints using standard likelihood ratio statistics. An alternative approach, more common in recent studies, is to employ Bayesian methods, which in particular allow to explicitly incorporate phylogenetic uncertainty in the analysis (Currie and Meade, 2014). Given the available sample of Austronesian language trees and following recent best practices, we rely on the reversible-jump Markov chain Monte Carlo (RJ MCMC) approach proposed by Pagel and Meade (2006). In this approach, MCMC methods are used to directly search among the numerous possible models of trait evolution, defined by the number of distinct transition rate parameters, and simultaneously estimate the posterior distributions of these rates while moving around the available sample of phylogenies. Another advantage of this method is that it avoids overparameterization by settling on the most parsimonious models providing good fit for the data. At stationarity, a converged Markov chain samples from the posterior distribution of models of trait evolution and the parameters of these models.

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<sup>14</sup>Note that the phylogenetic logistic regression model from previous section relies on the same assumptions in the first stage of the evolutionary process for the binary outcome variable.

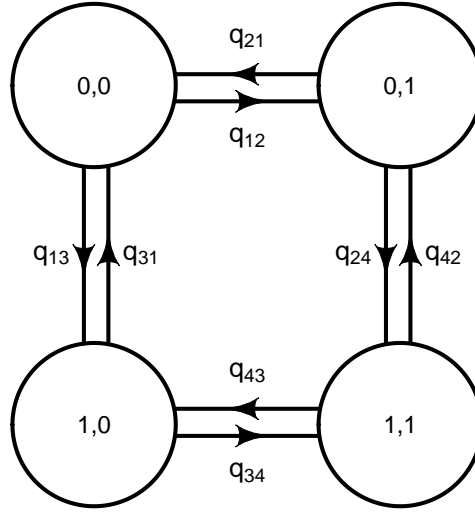


Figure 6: Transitions between states in the model of correlated evolution.

*Notes:* In our analysis, headhunting is the first trait and frequent warfare is the second trait in the pair. Hence, in state (0,0), both headhunting and frequent warfare are absent and in state (0,1), headhunting is absent but frequent warfare is present. Similarly, in state (1,0), headhunting is present but frequent warfare is absent and in state (1,1), both headhunting and frequent warfare are present. In a general model of correlated evolution, transition rates  $q_{ij}$  are not subject to any restrictions, but in a model of independent evolution, four pairs of rates must be the same:  $q_{12} = q_{34}$ ,  $q_{13} = q_{24}$ ,  $q_{21} = q_{43}$ , and  $q_{31} = q_{42}$ . Such conditions imply that the rate of change in each trait's value is unaffected by the value of the other trait. For example,  $q_{12} = q_{34}$  means that the rate of transition from infrequent to frequent warfare is the same whether headhunting is present or not, and  $q_{13} = q_{24}$  means that the rate of acquiring the practice of headhunting is independent of warfare frequency.

As with any MCMC estimation, there are several settings that need to be chosen to perform the analysis. In making these choices, we largely follow Watts et al. (2016) who employ the RJ MCMC method to explore the correlated evolution of human sacrifice and social stratification across Austronesian societies. We use uniform prior for models of evolution and exponential hyperpriors for transition rate parameters, with the range informed by ML estimates. Thus, before running the RJ MCMC analysis, we found ML estimates of transition rates for both independent and dependent evolution models for each of the 4,200 linguistic trees and computed their averages. These varied roughly from 0 to 0.3, and we accordingly set the hyperprior ranges to (0,0.4) to cover this interval for all rates. Each analysis was run for one billion iterations, with half of them discarded as a burn-in period to ensure convergence. We sampled from the chain every 10,000 steps to avoid autocorrelation between iterations. All computations were performed using BayesTraits software (Meade and Pagel, 2021).

In a Bayesian setting, hypotheses regarding correlated evolution and its directionality can be tested using Bayes factors (BF) defined as twice the difference between the log marginal likelihoods of the posterior distributions for two competing models (for example, unconstrained correlated versus independent evolution). We used a stepping-stone sampler with a  $\text{Beta}(0.4, 1)$  distribution to estimate the log marginal likelihood of each run, with 1,000 iterations across 100 stones (Meade and Pagel, 2021). We apply standard rules of thumb from Raftery (1996) when interpreting the magnitude of BF values: 0–2 as indicating no support for the first model (with a higher value of marginal likelihood) over the second one, 2–5 as positive evidence, 5–10 as strong support, and above 10 as very strong support.

### 5.2.2 Results

We start by running the RJ MCMC analysis for the unconstrained case allowing for any form of correlated evolution. The resulting posterior distributions of transition rates are shown in figure 7, along with the averages indicated by vertical lines. The distributions of  $q_{13}$  and  $q_{42}$  clearly stand out as these parameters are set to 0 in the vast majority of iterations. Other transitions rates have similar means and roughly bell-shaped distributions, with the exception of  $q_{43}$  which is set to 0 in 12% of sampled iterations. Indeed, the model of evolution visited most frequently (slightly more than 80% of the time) at the stationary distribution of the Markov chain is the one in which  $q_{13} = q_{42} = 0$  and the remaining rates are set equal to each other. In the second most frequently visited model (only 8% of the time),  $q_{43} = q_{42} = 0$ , with other rates set equal to each other. Table F.1 in the appendix lists the top ten models (out of 452 visited in total) accounting for 96% of the posterior sample.

Each row in figure 7 corresponds to the pairs of rates that must be identical in the independent evolution case. Striking differences between two pairs ( $q_{13}$  and  $q_{24}$ ,  $q_{31}$  and  $q_{42}$ ) suggest that models of correlated evolution dominate the posterior sample. A formal test confirms that there is strong support in favor of correlated evolution, with the value of BF exceeding 7. Thus, headhunting and frequent warfare coevolved.<sup>15</sup>

Figure 8 graphically shows the estimation results using the flow diagram. Here, solid connecting lines correspond to relatively high average transition rates (all similar in magnitude), whereas two dashed lines correspond to the average rates that are very close to zero.

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<sup>15</sup>The estimates of transition rates in our posterior sample allow us to implement the so-called ancestral state reconstruction, which evaluates the probabilities of a trait taking specific values at each node of the respective linguistic tree. We perform this procedure to illustrate the inferred evolutionary pathway of headhunting over time and report the results in appendix G.

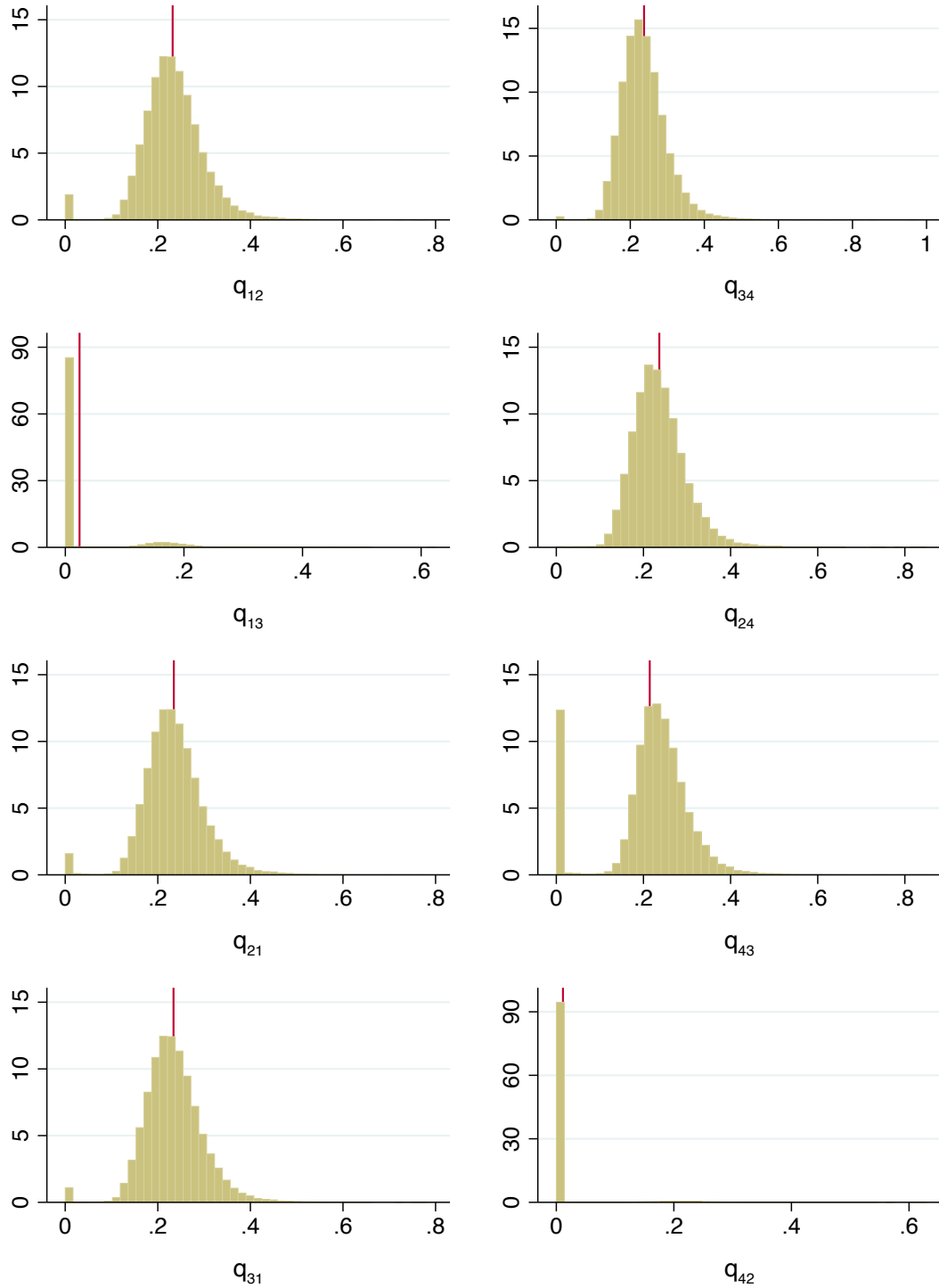


Figure 7: Posterior distributions of transition rates in the correlated evolution model.

*Notes:* The figure shows posterior distributions of transition rates in the unconstrained correlated evolution model estimated by the RJ MCMC method, based on 50,000 sampled iterations. Vertical lines mark the mean values. Each row corresponds to the rates that must be equal in the independent evolution case.

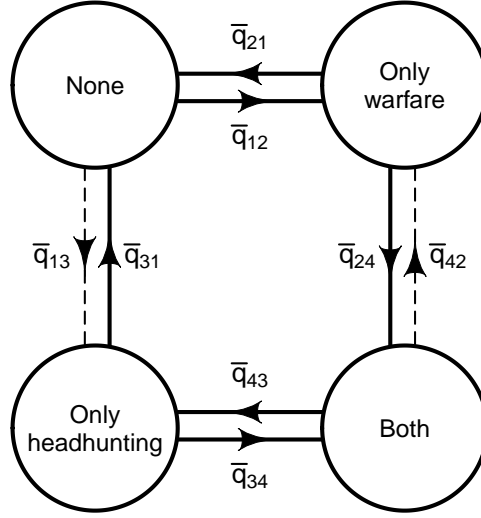


Figure 8: Average estimated transitions rates in the model of correlated evolution.

*Notes:* “Warfare” refers to frequent warfare. Dashed lines correspond to the average transition rates  $\bar{q}_{13}$  and  $\bar{q}_{42}$  that are both very close to zero. This means that gaining headhunting from a state with infrequent warfare and losing it from a state with frequent warfare are both very unlikely. Solid lines correspond to the remaining average transition rates that are all relatively high (and similar in magnitude). Thus, respective changes in trait values are substantially more likely than those marked by dashed lines.

This figure illustrates several interesting findings. First, frequent warfare appears to be all but prerequisite for gaining the practice of headhunting. The value of  $q_{13} \approx 0$  suggests that the adoption of headhunting is very unlikely from a state in which warfare is only occasional, rare, or non-existent. Second, reducing the frequency of warfare or eliminating it appears to be an important condition for losing the practice of headhunting. The value of  $q_{42} \approx 0$  suggests that its loss is very unlikely from a state in which both headhunting and frequent warfare are present. Third, changes in warfare frequency appear to be largely independent of headhunting, as implied by the similarity of the relevant pairs of transition rates ( $q_{12} \approx q_{34}$  and  $q_{21} \approx q_{43}$ ).

We formally test these hypotheses by running the RJ MCMC analysis after imposing appropriate constraints on transitions rates and comparing the resulting model fit to the baseline case of unconstrained correlated evolution. The types and results of these tests are summarized in table 3. The first sequence of four tests aims to suggest that headhunting was an adaptive cultural response to frequent warfare. We start with two basic hypotheses (rows 1 and 2) stating that the gain and the loss of headhunting are independent of warfare frequency. The constraint in row 1 equates the probabilities  $q_{13}$  and  $q_{24}$  of gaining headhunting from states with infrequent and frequent warfare, respectively. The constraint in row 2 does the same for the probabilities of losing headhunting. As shown in the last

Table 3: Testing hypotheses about the order of trait evolution

	Constraint(s)	Hypothesis	BF
(1)	$q_{13} = q_{24}$	H gain is independent of W	3.32
(2)	$q_{31} = q_{42}$	H loss is independent of W	4.39
(3)	$q_{13} = 0$	H gain impossible prior to W gain	-2.19
(4)	$q_{42} = 0$	H loss impossible prior to W loss	-2.32
(5)	$q_{12} = q_{34}$	W gain is independent of H	-1.00
(6)	$q_{21} = q_{43}$	W loss is independent of H	-0.63
(7)	$q_{13} = q_{42} = 0, q_{12} = q_{34}, q_{21} = q_{43}$	Joint	-6.88

*Notes.* H and W stand for headhunting and frequent warfare, respectively. Bayes factors (BF) are computed as twice the difference between log marginal likelihoods of the unconstrained and constrained models. Raftery (1996) suggests the following ranges for interpreting the absolute magnitude of BF values: 0–2 (no support), 2–5 (positive evidence), 5–10 (strong support), above 10 (very strong support). Negative BF values provide evidence in favor of the constrained model (null hypothesis), while positive values favor the unconstrained model.

column for rows 1 and 2, neither hypothesis is supported by the data. Instead, we find positive evidence (BF values between 2 and 5) in favor of the unconstrained model in which the evolution of headhunting is dependent on warfare frequency.

Next, we consider two stronger hypotheses about a particular order of trait evolution (rows 3 and 4). Specifically, the constraint in row 3 states that the probability  $q_{13}$  of gaining headhunting from a state with infrequent warfare is zero. Similarly, the constraint in row 4 states that the probability  $q_{42}$  of losing headhunting from a state with frequent warfare is zero. Bayes factors in rows 3 and 4, both exceeding 2 in absolute value, provide positive evidence in favor of these hypotheses. In other words, the data support constrained correlated evolution models in which the adoption and demise of headhunting follow, respectively, the rise and fall in warfare frequency.

In rows 5 and 6, we additionally test the hypotheses that the changes in warfare frequency are not conditioned by headhunting. Specifically, the constraint  $q_{12} = q_{34}$  in row 5 states that the probability of moving from infrequent to frequent warfare is the same whether headhunting is present or not. The constraint  $q_{21} = q_{43}$  in row 6 makes the same statement for the probability of a reduction in warfare frequency. These constrained models fit the data slightly better than the unconstrained model: although the BF values are not large enough to strictly prefer the former, there is definitely no support for the latter. Finally, as shown in row 7, the model imposing joint constraints specified in rows 3–6 is strongly preferred over the baseline of unconstrained correlated evolution (BF close to 7

in absolute value). Overall, the tests in table 3 indicate that the practice of headhunting evolved in response to changes in warfare frequency, consistent with the idea that it was a socially useful cultural adaptation to recurrent inter-tribal conflict. In contrast, there is no clear evidence that the dynamics of warfare frequency was conditioned by the presence or absence of headhunting.

We performed multiple sensitivity tests to confirm the robustness of our results. First, we ran each analysis three times to ensure that the results are consistent across runs, with standard Gelman and Rubin (1992) diagnostic indicating convergence. We doubled the number of iterations in the chain, half of it in burn-in phase, with results identical to the baseline. We experimented with different settings for the stepping-stone sampler and obtained very similar estimates of the relevant marginal likelihoods. Sampling every 1,000th iteration of the converged chain yields results that are very close to the reported baseline. Finally, we also examined sensitivity to assumptions on the prior distributions of parameters. We found very similar estimates for average transition rates when doubling the width of our baseline hyperprior interval and when assuming an alternative in which the mean and variance of the gamma prior are both seeded from a uniform hyperprior.

## 6 Concluding remarks

This paper examines the now-defunct practice of acquiring human heads for ritual use. Gruesome as headhunting was, we argue that it fulfilled an important social function. Specifically, the headhunting complex provided both a system of incentives for men to develop warfare skills by participating in risky raids and a way to verify the quality of their performance. In other words, it represented an effective mechanism for maintaining a regular class of trained men ready to protect their community from external threats. Such a mechanism should have been particularly useful in societies that were exposed to frequent warfare and, unlike most contemporary nations, lacked specialized military institutions and modern technologies to organize for warfare and monitor the performance of combatants.

We leverage phylogenetic comparative methods to empirically investigate this hypothesis in a sample of Austronesian societies. The evidence is consistent with our prediction: accounting for a range of confounding characteristics and cultural non-independence of observations, there is a strong positive relationship between warfare frequency and the presence of headhunting. Furthermore, estimates from correlated evolution models show that, in line with our hypothesis, increases in warfare frequency preceded the adoption of headhunting, but not the other way around. The demise of headhunting, in turn, followed the reduction in warfare frequency once the practice ceased to be socially useful.

# Appendices

## A Definitions of variables and summary statistics

The source of all original variables is *Pulotu* database, version 1.2 (Watts et al., 2022), with the exception of social stratification (Watts et al., 2016).

**Headhunting.** A practice of killing people for the sole or primary purpose of obtaining their heads. Coded as present or absent.

**Warfare frequency.** Frequency of lethal conflict with other societies, coded on the following ordinal scale: frequent, common, occasional, rare or never. The cutoffs separating these categories are one year, five years, and one generation. A binary indicator (frequent vs. infrequent warfare) is created by grouping the first two and the last two categories of the ordinal classification.

**Year of observation.** Approximate year to which ethnographic data on a particular society refer.

**Geographic isolation.** Natural logarithm of (one plus) the distance to closest landmass inhabited by a different culture (i.e., any culture other than the one being coded). If there was a different culture present on the same island, the distance is set to 0.

**Influence from major religions.** A binary variable equal to 1, if there is evidence of Christian, Muslim, Hindu, or Buddhist influence on local supernatural beliefs. Produced using three separate original variables.

**Population size.** Natural logarithm of the estimated population size.

**Political authority.** A right to manage interactions between living human beings, vested in a specific office and exercised over a specific group of people. Comprises the following categories: 1) absent, or restricted to a group no larger than the household; 2) sublocal (encompasses a group larger than the household but smaller than the local community); 3) local (encompasses the local community and/or multiple sublocal groups); 4) supralocal (encompasses multiple local groups).

**Social stratification.** Comprises the following three categories: 1) egalitarian (minimal or no potential for wealth and/or status to be inherited between generations); 2) moderate (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); 3) high (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).

**Reliance on agriculture for subsistence.** A binary variable equal to 1, if agriculture or horticulture were the principal source of food.

**Importance of land-based group hunting.** A binary variable equal to 1, if land-based hunting performed by one or more groups represented a non-minor source of food.

Table A.1: Summary statistics

	Mean	St. dev.	Min	Max	Obs.
Presence of headhunting, binary	.318	.468	0	1	107
Influence from major religions, binary	.225	.42	0	1	102
Reliance on agriculture, binary	.74	.441	0	1	104
Importance of land-based group hunting, binary	.284	.453	0	1	102
Year of observation	1881	53.1	1668	1983	107
Geographic isolation	2.09	2.52	0	8.2	107
Population size	9.02	1.79	4.13	13.5	101
<b>Warfare frequency, categories</b>					107
Rare or never	.374	.486	0	1	
Occasional	.262	.442	0	1	
Common	.187	.392	0	1	
Frequent	.178	.384	0	1	
<b>Political authority, categories</b>					103
Absent	.136	.344	0	1	
Sublocal	.0583	.235	0	1	
Local	.32	.469	0	1	
Supralocal	.485	.502	0	1	
<b>Social stratification, categories</b>					91
Absent	.209	.409	0	1	
Moderate	.495	.503	0	1	
High	.297	.459	0	1	

## B Spatial distribution of warfare frequency

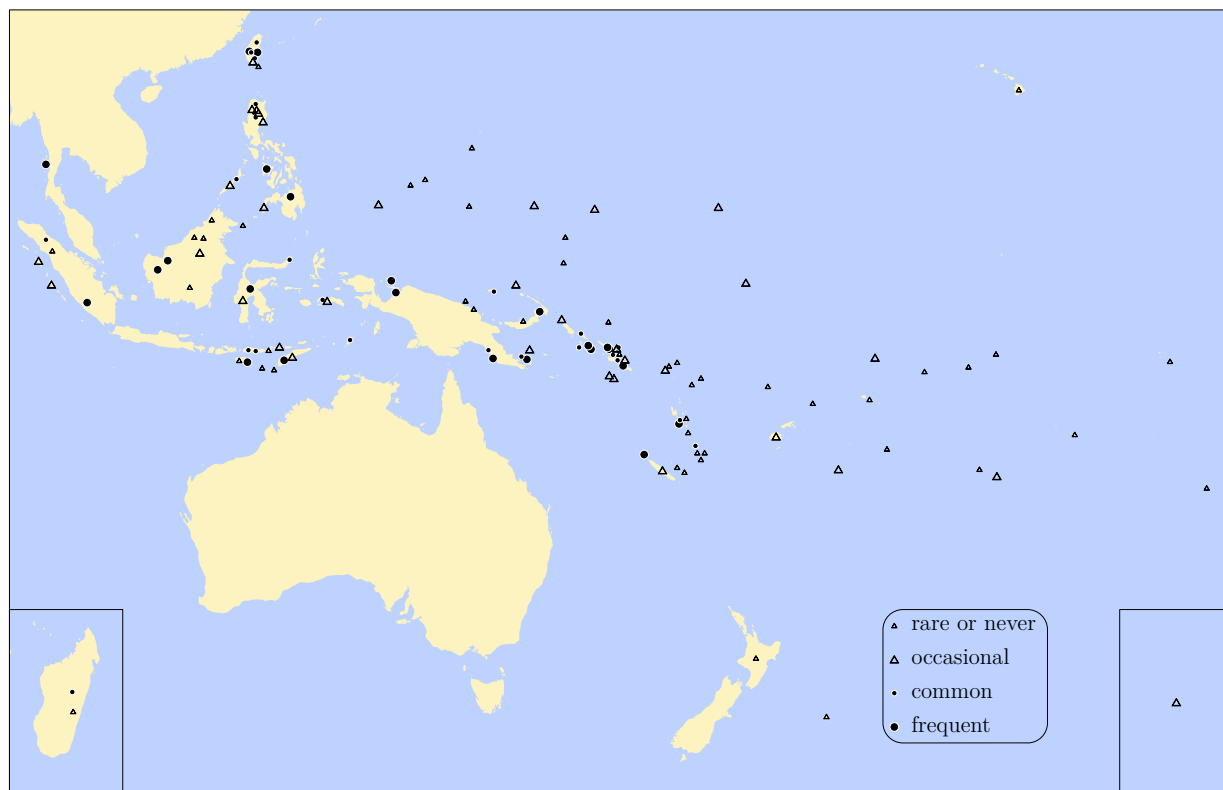


Figure B.1: Spatial distribution of warfare frequency across Austronesian societies.

*Notes:* The inset maps in the bottom-left and bottom-right corners show Madagascar and Rapa Nui (Easter Island), respectively. The hollow triangle marker is used for “rare or never” and “occasional” categories (which are grouped together as “infrequent warfare” in the analyses requiring a binary warfare variable). The solid circle marker is used for “common” and “frequent” categories (which are grouped together as “frequent warfare” in the analyses requiring a binary warfare variable).

## C The problem of cultural non-independence

This appendix illustrates the basic problem posed for standard statistical methods by cultural non-independence due to common ancestry. A simple example that follows has been adapted from Mace and Pagel (1994). For a further non-technical overview see Nunn (2011) and Mace and Zhang (2023).

Consider a sample of nine societies (labeled  $1, 2, \dots, 9$ ) that is used to explore the relationship between two binary traits, A and B. Suppose that both traits are present in four societies and both are absent in the remaining five. Standard statistical analysis

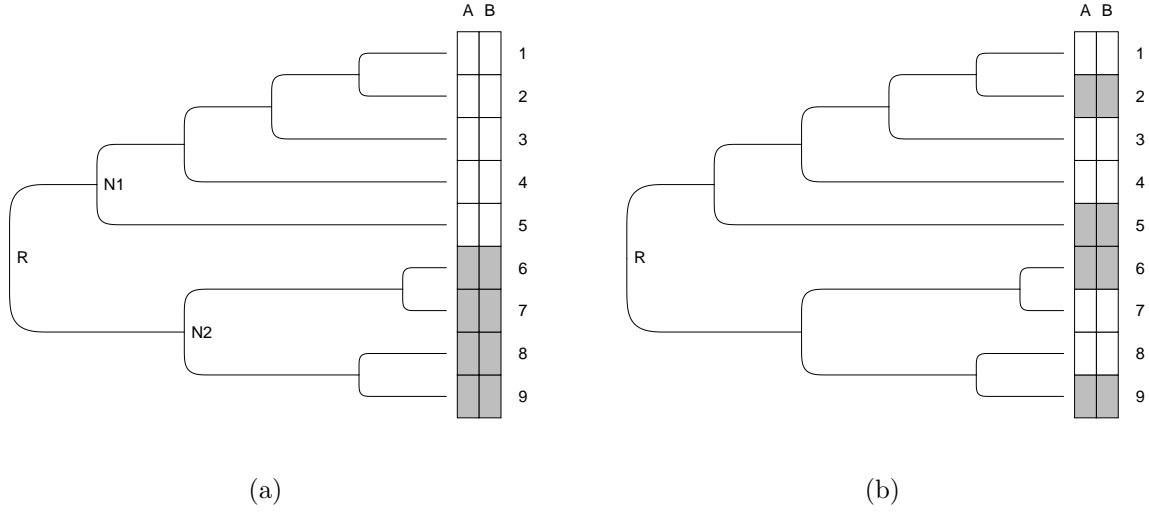


Figure C.1: Correlation between traits and cultural non-independence.

*Notes:* Adapted from Mace and Pagel (1994). Shaded cells indicate the presence of traits in respective societies. R marks the root of the tree.

would treat these nine societies as independent observations and conclude that there is a very strong association between traits A and B. Such correlation could then be described as consistent with a certain causal interpretation (for example, trait A representing an adaptive cultural response to trait B). However, this evidence may be weak if one accounts for non-independence of observations due to shared cultural ancestry.

Figure C.1 presents two hypothetical scenarios. In each case, data on traits A and B across nine societies are shown along with linguistic trees reflecting ancestral relationships between these societies. Shaded cells indicate the presence of traits. Both panels of the figure use the same tree, but depict alternative distributions of traits across societies for the purpose of illustration.

Consider panel (a) first. Traits A and B are absent in societies 1–5 and present in societies 6–9. As seen from the tree structure, the former five societies share the most recent common ancestor at node N1, while the latter four share the most recent common ancestor at node N2. Assume that cultural traits tend to be transmitted vertically across generations, as a result of which newly formed societies inherit a variety of traits from their ancestors. Furthermore, assume that both A and B are absent at the root of the tree (R), representing the common ancestor of all societies in the sample. Then, the observed distribution of traits across nine contemporary societies at the tips of the tree can be largely explained by plain cultural inheritance. For societies 1–5, the absence of both traits could have been simply inherited from the common ancestor at R and transmitted unchanged over

time. For societies 6–9, it is plausible that traits A and B became present somewhere on the tree branch between R and N2, following which they were both transmitted to “daughter” cultures and persisted to the observation period. Thus, the change in traits A and B may have only occurred once a long time ago, and their presence or absence in contemporary societies reflects the “mechanical” process of cultural inheritance. In this scenario, treating our sample of nine societies as independent observations (each contributing a piece of evidence on the relationship of interest) and ignoring their shared cultural ancestry would overstate the case for a strong association between A and B.

In panel (b) of figure C.1, trait bundles are “reshuffled” across societies, but the phylogeny remains the same. Note that in this case, nothing has changed from the perspective of standard statistical analyses treating observations as independent. There are still 5 societies with both traits absent and 4 societies with both traits present. Thus, the strength of measured association between A and B does not change compared to panel (a) scenario. However, a closer look at the pattern of ancestral relationships reveals additional useful information. For example, there are three pairs of “sister” societies (1 and 2, 6 and 7, 8 and 9) each sharing recent common ancestors but having different trait bundles. Thus, trait values must have diverged on these three separate occasions, providing stronger evidence for a functional relationship between traits A and B.

Phylogenetic comparative methods directly incorporate the information on cultural non-independence, contained in linguistic trees, into statistical analyses to provide more accurate inference about the association between traits. For example, phylogenetic regression methods (like the one used in section 5.1) posit a certain model of trait evolution along the branches of a linguistic tree and produce a generalized variance-covariance matrix of the error terms that is subsequently used in estimation. A different suite of methods (like the one used in section 5.2) exploits the linguistic tree structure, along with a posited model of trait evolution and the actual distribution of data at the tips of the tree, to estimate the most likely order of trait evolution in the past.

## D Standard logit estimates

Table D.1: Logit estimates

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
<b>Warfare</b>								
Occasional	2.357*** (0.826)	2.288*** (0.830)	2.187*** (0.848)	2.275*** (0.859)	2.301** (0.910)	2.061** (0.947)	2.221** (0.922)	1.991** (0.979)
Common	2.944*** (0.852)	2.971*** (0.862)	2.491*** (0.900)	2.378*** (0.897)	2.099** (0.933)	2.282** (0.959)	2.147** (0.974)	2.241** (1.029)
Frequent	3.483*** (0.867)	3.530*** (0.879)	2.893*** (0.932)	2.817*** (0.932)	2.726*** (1.009)	3.011*** (1.081)	2.674** (1.045)	3.367*** (1.225)
<b>Year of observation</b>		0.007 (0.006)	0.003 (0.006)	0.001 (0.006)	0.002 (0.007)	0.000 (0.007)	0.001 (0.007)	−0.000 (0.007)
<b>Geographic isolation</b>			−0.263* (0.141)	−0.313** (0.152)	−0.456** (0.185)	−0.565*** (0.203)	−0.412** (0.190)	−0.464** (0.216)
<b>Major religion</b>				−0.495 (0.605)	−1.586** (0.778)	−2.646*** (1.007)	−1.363* (0.785)	−2.497** (1.056)
<b>Population size</b>					0.452** (0.206)	0.529** (0.230)	0.421* (0.236)	0.394 (0.252)
<b>Political authority</b>								
Sublocal						0.125 (1.349)		0.845 (1.555)
Local						1.498 (0.949)		1.866 (1.169)
Supralocal						1.580 (1.009)		1.876 (1.203)
<b>Social stratification</b>								
Moderate							−0.001 (0.782)	
High							−0.146 (0.953)	
<b>Agriculture</b>								1.018 (0.942)
<b>Group hunting</b>								0.783 (0.786)
Observations	107	107	107	102	96	92	85	88

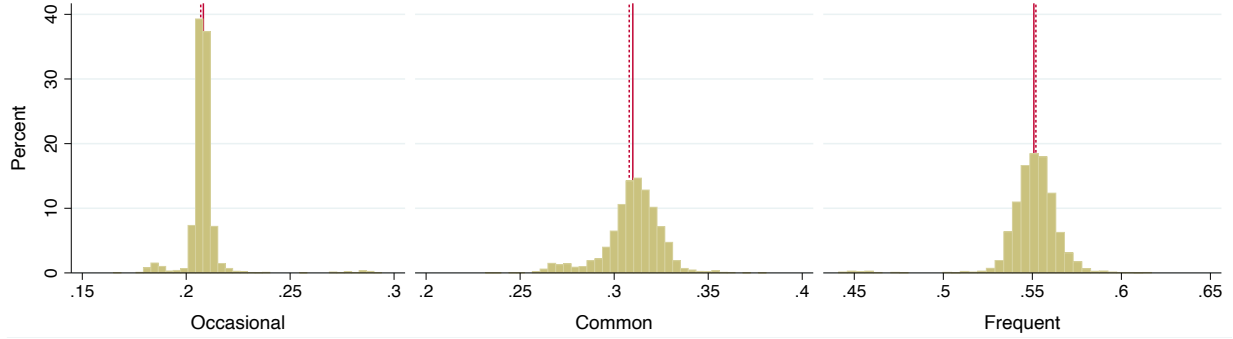
*Notes.* Dependent variable is the presence of headhunting. Omitted categories are: “rare or never” for warfare, “absent” for political authority and social stratification. \*\*\*, \*\*, and \* denote statistical significance at the 1, 5, and 10 percent level, respectively.

Table D.2: Average marginal effects for warfare frequency (standard logit)

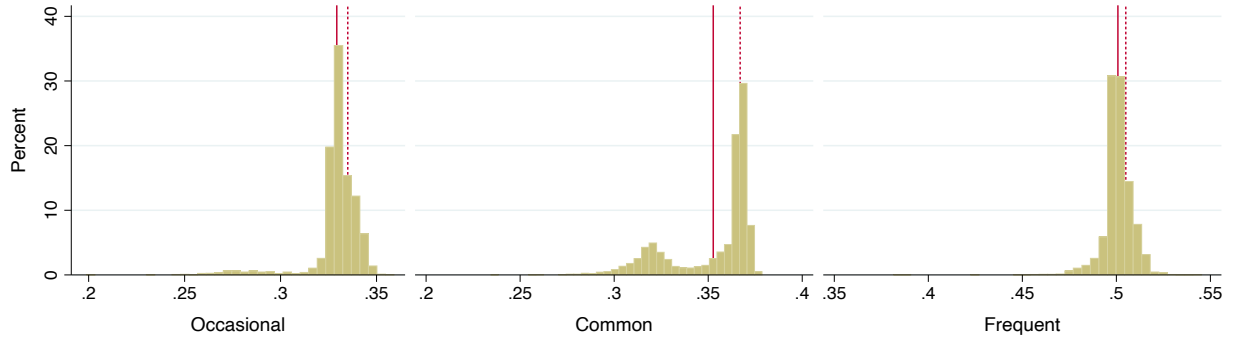
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Occasional	0.307*** (0.097)	0.289*** (0.094)	0.295*** (0.099)	0.326*** (0.105)	0.318*** (0.108)	0.262** (0.114)	0.333*** (0.118)	0.244** (0.117)
Common	0.450*** (0.117)	0.448*** (0.115)	0.360*** (0.117)	0.348*** (0.117)	0.282** (0.114)	0.300** (0.118)	0.319** (0.133)	0.286** (0.133)
Frequent	0.582*** (0.116)	0.580*** (0.113)	0.449*** (0.132)	0.444*** (0.133)	0.395*** (0.142)	0.429*** (0.152)	0.418*** (0.158)	0.483*** (0.170)
Observations	107	107	107	102	96	92	85	88

*Notes.* Omitted category is “rare or never.” \*\*\*, \*\*, and \* denote statistical significance at the 1, 5, and 10 percent level, respectively.

## E Phylogenetic uncertainty in regression estimates



(a) Specification 3 from table 1



(b) Specification 6 from table 1

Figure E.1: Average marginal effects of warfare frequency in a sample of phylogenetic trees.

*Notes.* The figure shows the distributions of average marginal effects of warfare frequency, estimated via the phylogenetic logistic regression model from section 5.1 for 4,164 Austronesian language trees from Gray et al. (2009). Of the original 4,200 trees, 36 (less than 1%) were dropped due to non-convergence of the estimation algorithm. Solid vertical lines correspond to the mean values and dashed lines mark the estimates from table 2 corresponding to the default (maximum clade credibility) linguistic tree.

## F Details of the correlated evolution analysis

Table F.1: Top ten models in the posterior sample

Model	$q_{12}$	$q_{13}$	$q_{21}$	$q_{24}$	$q_{31}$	$q_{34}$	$q_{42}$	$q_{43}$	Frequency	Percent	Cumulative
1	×	0	×	×	×	×	0	×	40,264	80.53	80.53
2	×	×	×	×	×	×	0	0	4,126	8.25	88.78
3	×	0	×	×	×	×	×	×	1,535	3.07	91.85
4	×	×	0	×	×	×	0	0	559	1.12	92.97
5	×	×	×	×	×	×	×	0	350	0.70	93.67
6	×	×	×	×	×	×	0	×	350	0.70	94.37
7	×	0	×	×	0	×	0	×	244	0.49	94.86
8	0	×	×	×	×	×	0	×	226	0.45	95.31
9	0	×	×	×	×	×	×	0	174	0.35	95.66
10	0	×	×	×	×	×	×	×	159	0.32	95.98

*Notes.* RJ MCMC analysis of the unconstrained correlated evolution model. 0 indicates a transition rate set to zero and × indicates equal non-zero rates.

## G Ancestral state reconstruction

We follow the method of Pagel et al. (2004) to probabilistically reconstruct the ancestral states for headhunting based on the analysis of section 5.2. This can be done for the root and internal nodes of any linguistic tree, given the estimates of transition rates. As mentioned in the main text, a particular advantage of Bayesian MCMC approach is that it takes into account phylogenetic uncertainty by allowing the Markov chain to sample linguistic trees from the available set instead of focusing on a specific phylogeny. As a consequence, our posterior sample contains linguistic trees that have different sets of internal nodes, which slightly complicates the presentation of our estimates.

We use the maximum clade credibility consensus tree, first shown in figure 3, to succinctly summarize our results following the approach of Watts et al. (2016). Specifically, we display average probabilities of the two states of headhunting (present and absent) at each node of this consensus tree. Note that, for a given node, these probabilities can only be estimated for the iterations of our posterior sample selecting trees in which that node is present.<sup>16</sup> For each node, we also record the share of iterations in which it is absent

<sup>16</sup>Here, a node is defined solely by the set of languages belonging to the clade originating from that node. Specific topology of the clade and its location on the tree do not matter.

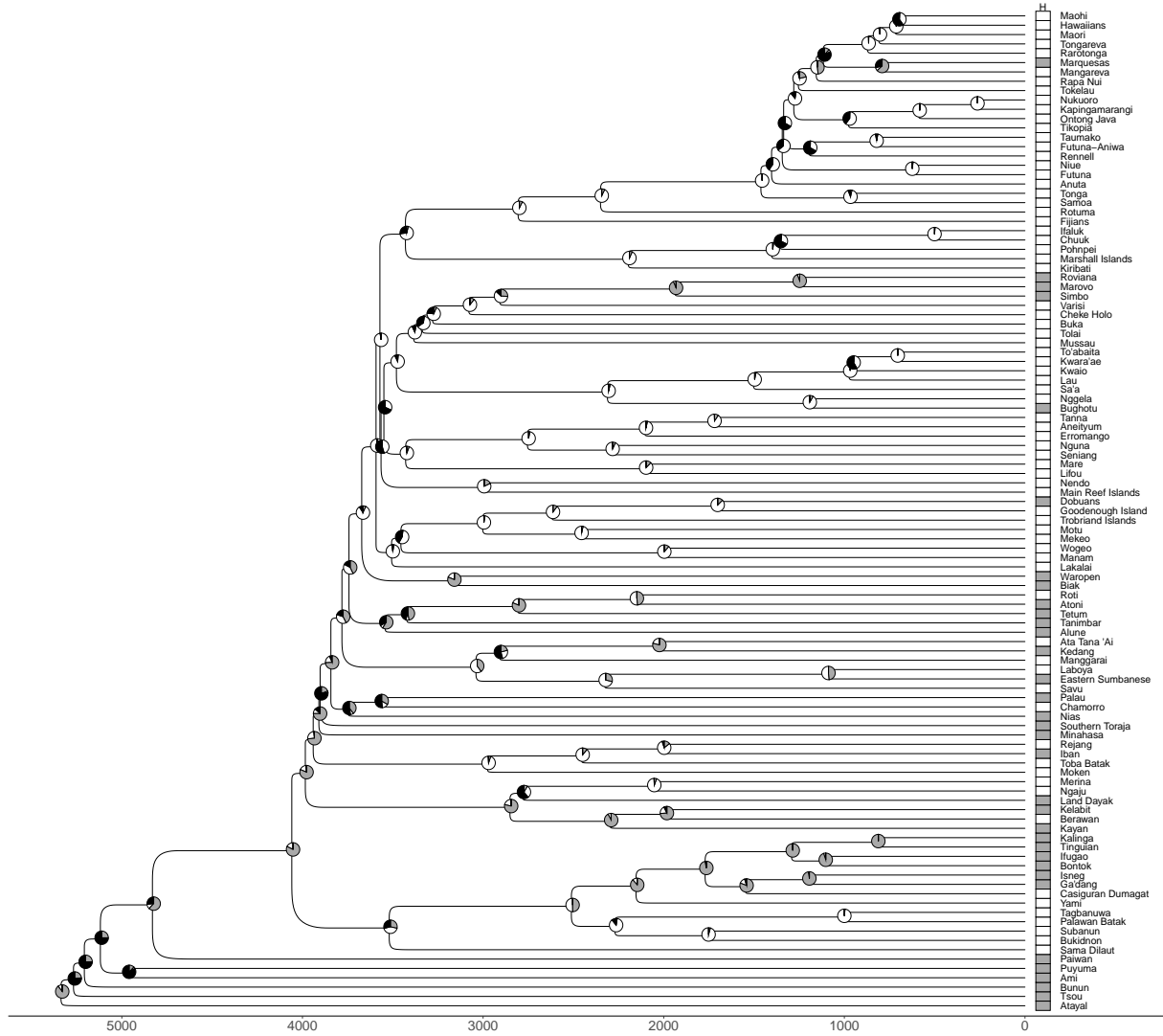


Figure G.1: Ancestral state reconstruction for headhunting.

*Notes.* This figure displays the results of ancestral state reconstruction for headhunting based on the posterior sample from the unconstrained correlated evolution analysis of section 5.2. These results are summarized using pie charts placed at the nodes of the maximum clade credibility consensus tree of Austronesian languages. Black sectors of the pie charts represent the share of iterations in the posterior sample selecting trees in which that internal node is absent (phylogenetic uncertainty). The remaining share of each pie chart is split between gray (average probability of headhunting being present) and white (average probability of headhunting being absent). As in figure 3, names of societies are listed at the tips of the tree and shaded cells indicate the presence of headhunting (H) in respective societies at the time of observation. Horizontal axis represents time measured in years before present.

(reflecting phylogenetic uncertainty). All relevant information is then shown in the form of pie charts placed at consensus tree nodes.



The results are shown in figure G.1. Black sectors of the pie charts represent phylogenetic uncertainty, while the remaining share of each pie chart is split between gray (average probability of headhunting being present) and white (average probability of headhunting being absent). The pie chart at the root of the tree indicates an average probability of 89% that headhunting was practiced by the ancestors of all Austronesian people more than 5,000 years ago.<sup>17</sup> From this likely ancestral state, headhunting evolved following the spread of Austronesians throughout the region and was lost and gained multiple times over their entire cultural history. For example, according to our reconstruction, after apparently being lost, the practice re-emerged in the ancestral cultures of the Roviana, Marovo, and Simbo (Solomon islands) and Waropen and Biak (New Guinea). In some cases, the ancestral state is highly uncertain: for instance, the internal node giving rise to a clade of societies residing largely in what is now the Philippines (located in the lower part of the tree between Bukidnon and Kalinga) is equally split between “present” and “absent” states.

Our results from section 5.2 suggest that the evolution of headhunting was influenced by the dynamics of warfare: the loss and gain of the practice typically followed, respectively, the reduction and increase in warfare frequency.

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<sup>17</sup>Each linguistic tree in our sample has a root, which explains why the corresponding pie chart does not have a black sector. In contrast, the existence of four “early” internal nodes at the bottom of the tree, capturing the branching of Formosan cultures, is very uncertain.

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