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The evolution of cultural diversity in Pama-Nyungan Australia

Duncan Learmouth[1]✉, Robert. H. Layton[1] & Jamshid. J. Tehrani[1]

Explaining the processes that produce cultural diversity has long been a focus of anthropological study. Whilst linguistic diversity has frequently been shown to be associated with population splitting during migrations, much less is known about the influence of migration patterns on other forms of culture. Here we compare variation between different cultural types to understand whether their diversity might also be a consequence of historic population change. For our case study, we developed a dataset of 90 cultural traits recorded across around 100 societies in Pama-Nyungan Australia focusing on three cultural forms important in Australian life: adolescent initiation, mortuary practice and rock art motifs. Trait diversity was analysed using phylogenetic methods and compared with language diversity since previous studies have suggested an association between Pama-Nyungan language evolution and population dispersal. We were able to demonstrate a strong association between the phylogenetic history of language and initiation ritual but not between language and mortuary ritual or rock motifs. The finding suggests population migration may have had a significant influence on initiation ritual diversity. It also lends support to the idea, as suggested by some authors, that the development of complex initiation practices may have played an active role in the dispersal of Pama-Nyungan speakers throughout the Australian continent. Our study results suggest that the type of phylogenetic comparative approach applied here can make an important contribution to the reconstruction of deep cultural history over long timescales.

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[1] Durham Cultural Evolution Research Centre, Department of Anthropology, Durham University, Durham, UK. ✉email: duncan.learmouth@durham.ac.uk

Introduction

The diversity and complexity of human culture manifests itself through multiple forms of language, ritual, myth, material objects, art, music, etc. Over the last two decades, a number of researchers have explored the origins of this diversity using phylogenetic methods that were originally developed to study the 'descent with modification' of biological species. For example, phylogenetic analysis has been widely used to investigate the history of language families by reconstructing changes in word forms that occur when speech communities split and gradually diverge from one another (Bowern, 2018). This process is often linked to population dispersals, providing powerful insights into the prehistory of a number of major population expansions such as Indo-European (Bouckaert et al., 2012), Bantu (Grollemund et al., 2015), Austronesian (Gray et al., 2009) and Pama-Nyungan (Bouckaert et al., 2018). Phylogenetic methods have also been applied to other cultural forms to infer histories of manuscripts (Barbrook et al., 1998), folktales (Tehrani, 2013; Da Silva & Tehrani 2016; Ross et al., 2013), musical instruments (Tëmkin, Eldredge (2007); Aguirre-Fernández et al., 2021) and material objects (Tehrani & Collard, 2002; Buchanan, Collard, 2007; Jordan & Shennan, 2009). However, most of these latter studies have tended to focus on a single cultural tradition, rather than addressing the evolution of cultural diversity as a whole or the question of how far different kinds of traits follow the same evolutionary paths (Mace & Holden, 2005; Tehrani et al., 2010; Riede, 2009). In this paper, we present a case study that investigates the evolution of cultural diversity by systematically comparing phylogenies derived from multiple cultural datasets of the Pama-Nyungan peoples of Australia.

Pama-Nyungan is the largest language family in Australia, whose speakers are believed to have dispersed across the continent 4000 to 7000 years ago (Bouckaert et al., 2018). These societies have a number of characteristics that make them a suitable choice for a comparative study of cultural diversity. Complex ritual practices play a central role in Australian life (Berndt & Berndt, 1996: p. 150) and ceremonial forms vary considerably between societies, allowing for meaningful comparisons to be made. A Pama-Nyungan linguistic history or phylogeny has been derived from existing language variation which suggests that these speakers were part of a dispersal process (Bowern & Atkinson, 2012; Bouckaert et al., 2018) and provides us with the opportunity to use language as a proxy for population migration. Some authors have suggested that Pama-Nyungan dispersal could be related to the development of multi-purpose stone tools and new food production techniques (Lourandos, 1997; Hiscock, 2007). Cultural factors have also been put forward as a mechanism for expansion, in particular the development of outward-reaching social alliances supported through a combination of expanded kinship systems and the introduction of collaborative ceremonial activity (Layton, 1992; Evans & Jones, 1997; Evans & McConvell, 1998; McConvell, 2001). Comparing the histories of cultural forms, such as ceremonial practices, with language may contribute to a deeper understanding of the reasons behind Pama-Nyungan expansion. Much less is known about why hunter-gatherer language dispersals like Pama-Nyungan may have taken place and their examination may help us understand more about the cultural changes that shaped early human history (Anthony, 1990; McConvell, 2001; Bellwood, 2013).

To investigate the evolution of Pama-Nyungan cultural diversity we plan to infer and compare different cultural histories. To do this, we need to consider whether their coherence over time has been sufficient to enable their phylogenetic reconstruction (Durham, 1992; Boyd et al., 2005; Tehrani & Collard, 2013). On the one hand, we might consider cultural forms to be integrated systems of traits (relating to symbols, ceremony and meaning) that only make sense together, e.g. as part of a system of belief. Such traits may be highly specified to the cultural tradition, resistant to transmission between neighbours and maintained their coherence over time. On the other hand, traits could be subject to relatively high levels of borrowing. For example, people may seek ways of improving representations of complex meanings and beliefs by copying novel ideas from neighbours. Repeated contact between groups, due to inter-marriage or exchange networks for example, might lead to a general drift towards cultural similarity, due to a desire to co-ordinate ritual practices or perhaps because of conformist bias (Boyd & Richerson, 1985; Mesoudi et al., 2004). In such a situation we would expect limited coherence over time and that phylogenetic reconstruction may not be feasible. In Australia, ethnographers have noted the transmission of cultural elements between neighbouring societies during the colonial era including rock motifs (Layton, 2003; Elkin, 1952), mythical narratives (Berndt, 1951a, 1951b; Elkin, 1961) and decorative items (Akerman & Stanton, 1994; Haynie et al., 2014). However, other cultural domains appear to have been relatively unaffected by diffusion such as ritual practices (Meggitt, 1966; Berndt & Berndt, 1996: p. 169; Elkin, 1961: p. 202). This background suggests we should expect a mix of influences on Australian cultural diversity and we have adopted a study design that accommodates these effects.

After collecting and coding data on ritual traditions and rock art motifs (see below), we reconstructed their transmission histories using a Bayesian, character-based method, *Mr Bayes* (Huelsenbeck & Ronquist, 2001). This assumes trait change has been driven by the branching process we would expect if cultural traditions developed along an evolutionary or 'descent with modification' pathway. We then analysed the same data using a distance-based network method *Neighbour Net* (Bryant & Moulton, 2004) to understand the extent to which data conflict with a bifurcating tree model. Areas of conflict in the network may reflect the effects of trait diffusion or borrowing between neighbours.

Next, we examined the coherence of each tradition by evaluating the role played by processes of cultural descent and diffusion. Firstly, using language as a proxy for cultural descent, we investigated the phylogenetic signal of each trait (Fritz & Purvis, 2010). Secondly, using geographic proximity as a proxy for diffusion, we used autologistic modelling to analyse the combined effects of language and geography on trait variation (Towner et al., 2012).

Data preparation

Phylogenetic methods model history by breaking down the cultural entity into units of transmission that demonstrate both continuity and variation across populations. Here, we analyse each form in terms of its constituent traits; aspects of cultural practice with continuity and variation across the Pama-Nyungan region. No large-scale, quantitative analysis of Australian culture has been carried out before and a substantial part of this study has involved the collation of ethnographic material into a form suitable for quantitative analysis. The dataset was required to be large enough for the application of quantitative models and have sufficient relevance, in terms of the importance of the cultural form, to support meaningful conclusions with respect to Pama-Nyungan cultural history. We anticipated that important cultural forms would also have a higher likelihood of being conserved over time. Furthermore, we wanted to examine traits associated with ceremonial activity as this has been theorised as a possible mechanism of Pama-Nyungan expansion (as discussed above). As the study is comparing culture with language, we also needed to be able to assign the trait data to language groups. Finally, in more practical terms, sufficient cultural material needed to be available. Taking account of these criteria, three cultural forms were chosen for inclusion: adolescent initiation rituals, mortuary practices and rock art motifs.

Initiation rites. Adolescent initiation is probably the most significant ceremony in Australian life, frequently involving complex settings, multiple age-stages and painful ordeals and mutilations (Berndt & Berndt, 1996). Ceremonies take place for both males and females beginning around puberty with male ceremonies tending to have wider social participation, more intricacy and a greater focus on the acquisition of knowledge, particularly religious knowledge. Because of the additional complexity, and probably because ethnographers have tended to be male, more material exists for male ceremonies and these have a greater focus in the dataset. Male initiation has a similar general pattern across the region: the novice is removed from the main camp and segregated, transition rites are performed and secret knowledge is revealed, the boy then returns to camp as an adult.

Ceremonies are highly collaborative with ancestral myths and narratives commonly enacted, accompanied by dance and music, in performances taking place over many hours and sometimes days. The novice is normally painted first and there may be a ceremony of release by the women of the camp. Separate rites are then performed including ordeals and painful mutilations such as circumcision, sub-incision (a deep cut along the underside of the penis), tooth removal and scarification. These often take place in a demarcated sacred ground that may contain various earthworks and platforms. Afterwards, boys may be segregated for long periods of time, sometimes many months, before being permitted to return to camp with the new status of an adult. Girls may also be segregated but for a shorter period, often related to menstruation. Readmission, as an adult male or female, maybe marked with new styles of body painting, hair decorations and gifts such as spears, shields, armbands and human hair belts.

Initiation practices were observed frequently during the late 1800s and recorded in publications by authors including Mathews (1894–1917), Spencer & Gillen (1899–1904), Howitt (1904) and Roth (1897–1910), see S1. This information provides the core material for the dataset with Greenway's 1963 bibliography providing additional sources. In total, 92 publications from 21 different authors were used and material from most of Pama-Nyungan Australia is included, with the exception of Western Australia. The focus of the study is on this early work because of the greater number of communities for which material is available and because there was less impact from European contact. Later authors also made detailed accounts but by this time many communities had suffered such severe disruption, including forced relocation away from their homelands, that interpretation of this material is difficult. In particular, it becomes challenging to allocate practices to specific linguistic groups which is a key requirement of this study.

Whilst all material in the dataset has been previously published, in most cases, this took place over 100 years ago and it is important to address ethical considerations associated with its re-use. There is sensitivity concerning 'secret-sacred' material, defined as rites, songs and objects only accessible to specific people, based, for example, on their clan membership, age or gender (Gibson 2019). In this study, only generalised ritual traits have been re-published and descriptions of ceremonies and mythical names and narratives are excluded. Traits are considered generalised if they have been extensively characterised in the public domain, for example in widely read publications such as Berndt & Berndt's *The World of the First Australians (1996)*. Two traits (see below) did not meet these conditions and have been anonymised (as ordeal1 and ceremony1).

Whilst data has been collated from a specific period (1850–1910), factors such as European expansion, seasonal variation and observer error or oversight might lead to reporting variation between societies. To address this, traits were only selected if they tended to be regularly recorded by the different authors. Societies with very low numbers of attributes (10 or less) were also excluded. Focus was given to achieving a representative mix of ceremonial, e.g. performance, and physical, e.g. genital mutilation and, as far as possible, traits were selected that were independent of one another. If they co-vary this is likely to obscure any underlying signal in the phylogenetic reconstruction (Nunn, 2011). Material was allocated to linguistic groups using information contained in the ethnography (see S1). References to language and location were cross-checked for accuracy using the language database *Austlang* (https://collection.aiatsis.gov.au/austlang). In total, the presence or absence of 27 initiation traits was recorded across 109 linguistic groups, see Fig. 1 for locations and Table 1 for the trait list.

Mortuary practices. Death and burial customs play an important role in Australian societies, often involving large numbers of mourners and the use of symbolic elements such as grave markings, body disposal methods and later rituals associated with the bones of the deceased (Berndt & Berndt, 1996). Practices reported vary across the continent, particularly in the way the corpse is prepared and the methods of its disposal. Ceremonies tend to be more complex in the north with elaborate song cycles, specially prepared grounds and later secondary rites. Desiccation of the body, sometimes as a result of tree or platform disposal, and often followed by these rites, is common in the north and also in parts of the southeast. Preparation of the corpse, for burial or other disposal methods, takes various forms including wrapping the body, tying hands, the removal of hair and nails etc. These are commonly explained as measures to prevent the corpse from causing trouble for the living before it has been avenged (Berndt & Berndt, 1996).

The only continent-wide analysis of the Australian mortuary ritual is from Meehan (1971). Examining a wide range of ethnographic material, Meehan first distinguished between the presence of simple (one stage) and compound (two or more stages) corpse disposal. These two methods were then further analysed. For simple disposal, whether this involved trees, platforms, cremation or burials, etc. and then additional variants were identified based on the preparation of the corpse, the grave, grave surroundings, etc. Compound disposals were further analysed based on the first step of the practice, whether this was drying, elevation, burial, etc. Using this approach 98 attributes were identified. Recording did not overlap so, for example, the presence of simple burial and burial as the first step in compound disposal were two separate observations. Sources included more recent material than for initiation, however a much greater proportion of observations came from earlier accounts. Potential bias from later material does however need to be borne in mind, particularly the encouragement of simple burial and the discouragement of compound and tree disposal by Christian missionaries.

To select the traits for analysis, similar criteria were applied as to those used for initiation with traits identified based on variability, independence and breadth. Many of the 98 attributes were either too infrequent, could not be clearly categorised or lacked independence. Following these adjustments, a total of 26 traits were selected for phylogenetic analysis (see Table 1) across 136 linguistic groups (Fig. 2). See S2 for more details of the trait

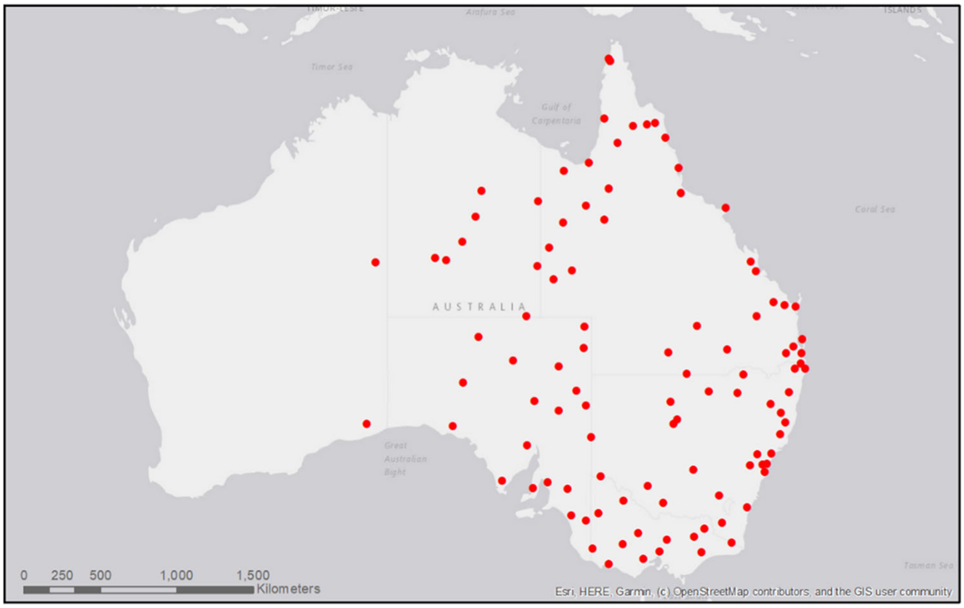


Fig. 1 Location of 109 Pama-Nyungan societies with initiation data.

Table 1 List of 90 cultural traits used in phylogenetic analysis (in alphabetical order). Starred traits (*) had significant phylogenetic signals (after accounting for geographic proximity), see section 'Comparison with geography and language'.

Initiation traits		Mortuary traits		Rock motifs	
1	barkBeating*	1	CorpContracted*	1	animatedHumanForms*
2	beginRed*	2	CorpMutilate	2	arcs
3	ceremony1*	3	CorpTied	3	barredCircles
4	circumcision*	4	CorpWrapped*	4	barredRectangle
5	eldersBlack*	5	CpdDisposalAll*	5	birdFootprints
6	endWhite*	6	CpdDisposalBurial*	6	birdForms
7	extendSubIncision*	7	CpdDisposalCannibal	7	circles
8	femaleFinger*	8	CpdDisposalDrying*	8	concentricArcs
9	femaleFire*	9	CpdDisposalElevation	9	concentricCircles
10	femaleGenMutilation*	10	CpdDisposalRetention	10	crossForms
11	femaleHairBelt*	11	GraveCarvedTree	11	curvedMazeForms
12	femaleScarification*	12	GraveClearing	12	dots
13	femaleTooth*	13	GraveDeep	13	faceForms
14	fireOrdeal*	14	GraveFires*	14	fishForms*
15	hairBelt*	15	GraveGoodsIn	15	humanFootprints*
16	hairDesign*	16	GraveGoodsOn*	16	humanForms
17	hairRemoval*	17	GraveHut	17	ladderForms
18	highSegregation*	18	GraveMortuaryItems*	18	lizardHumanForms
19	highStages*	19	GraveMound	19	macropodFootprints
20	humanPlatform*	20	GraveNiche	20	macropodForms*
21	ordeal1*	21	GraveStructure	21	mammalFootprints
22	processional*	22	GraveVegetation	22	mammalForms
23	scarification*	23	SimpleBurial	23	mazeForms*
24	subIncision*	24	SimpleCannibal	24	parallelLines
25	toothAvulsion	25	SimpleCremate	25	rakeForms
26	tossingRite*	26	SimpleTree*	26	reptileForms
27	treeClimbing*			27	rings
				28	shipForms
				29	silhouetteForms
				30	snakeForms
				31	starForms
				32	stemmedCircles
				33	treeForms
				34	tridents
				35	turtleForms*
				36	wishboneForms
				37	zigZags

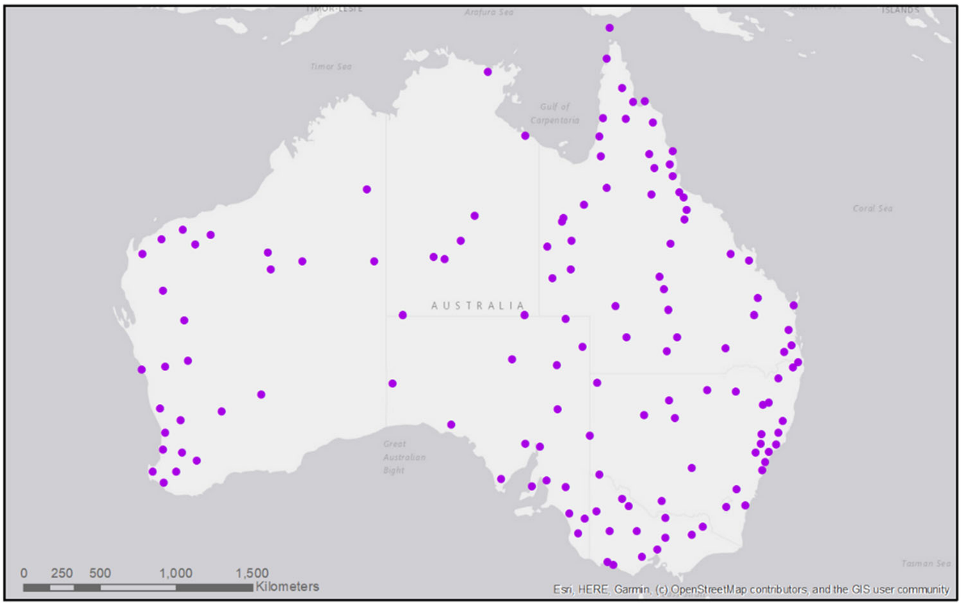
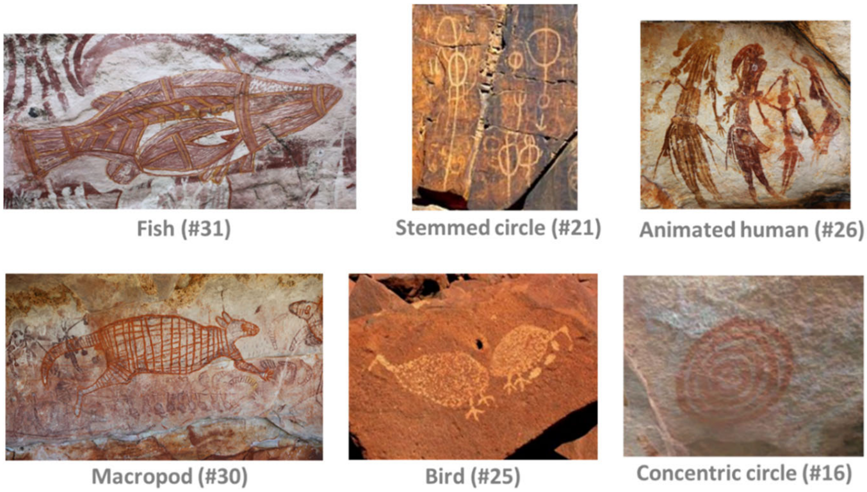


Fig. 2 Location of 136 Pama-Nyungan societies with mortuary ritual data.


Fish (#31)

Stemmed circle (#21)

Animated human (#26)

Macropod (#30)

Bird (#25)

Concentric circle (#16)

Fig. 3 Examples of recorded rock art motifs. Reference numbers (#) are as listed in the supplementary dataset (S3b).

selection and allocation process. As with initiation, there is good geographical coverage but with added representation from Western Australia.

Rock art motifs. Australia has many hundreds of sites containing rock paintings and engravings and they represent an important archive of Indigenous cultural history. Paintings involve the application of pigment, such as red and yellow ochres, to the rock surface. Engraving is done either by chipping away surface levels of rock or using a tool to incise markings. Although cave paintings and engravings can be very ancient most Australian images have been created in more recent history and can even be regarded as a contemporary practice in some areas. Layton (1992) documented 40 reports of active rock painting and engraving between 1830 and 1986 across the continent. Paintings in a number of areas contain representations of Europeans and artefacts such as ships, horses and guns. The relatively recent age of many images suggests that it is a reasonable assumption to assign them to the linguistic groups in that location in the ethnographic record, subject to adjustments for rock art that is known to be particularly ancient (see S3a for an explanation of dataset adjustments). This contemporary nature also means that something of the meaning and context of the images has been preserved, both through discussion with Indigenous people and comparison to ethnographic accounts. Images are often connected to religious belief in some way (Maynard, 1975) and may be directly incorporated into rituals (Layton, 1992: p. 47), form part of ceremonial grounds (McBryde, 1974) or illustrate legendary characters (Elkin, 1949). Images may also have a didactic role, encompassing both religious and secular aims. For example, depictions of journeys by Dreamtime beings can also indicate optimal walking tracks between water holes or foraging routes (Elkin, 1934; Layton, 1992). Animal paintings can illustrate the abundance of species and the ways in which they should be killed and eaten (*ibid*, 74) but, when combined with particular infill patterns, take on a sacred role that also signifies clan membership and territorial allegiance. Authors have often distinguished between the presence of so-called figurative or representative designs and geometric or more abstract patterning. Layton (1992) suggests a number of changes in Australian rock

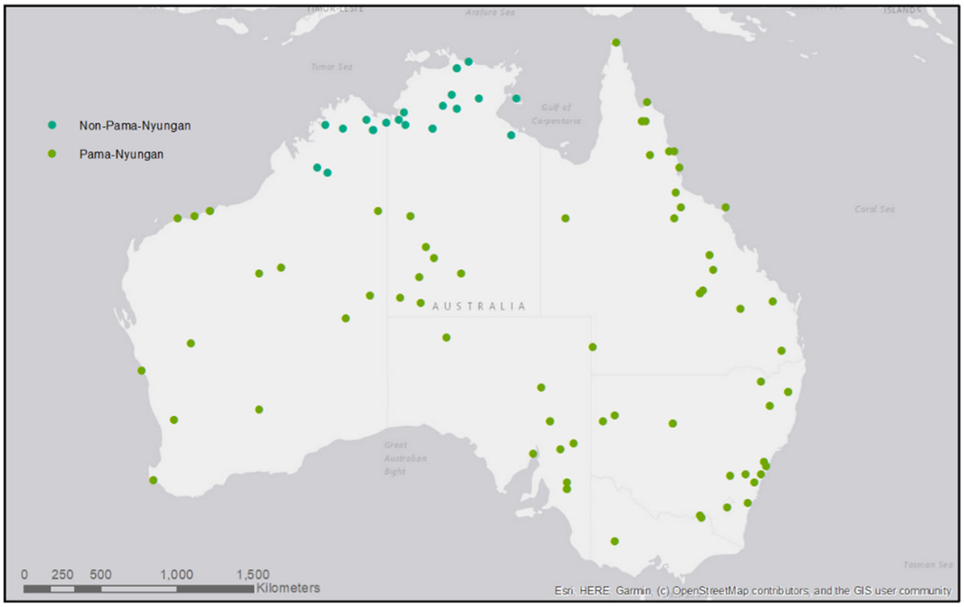


Fig. 4 Locations of 97 sites (both Pama-Nyungan and Non-Pama-Nyungan) included in the rock motif dataset.

art that may be linked to the development or use of geometric designs such as an expansion of these motifs in parts of South East Australia *(ibid*, 227) and Queensland (*ibid*, 241), and this type of design becoming more sacred in Central Australia *(ibid*, 236–7).

Previous analyses of Australian rock images have identified particular motifs, or certain arrangements of shapes, which recur within stylistic regions that may signify the cultural group of the artist (Maynard, 1977). The use of motifs as building blocks to assemble more complex meanings is supported by ethnographic analysis such as Munn's detailed accounts of Warlbiri imagery (1973) and researchers have been able to discern motifs recurring in multiple locations that may be suggestive of a shared cultural history. Building on this work, Layton analysed the presence/absence of 37 such motifs across over 100 locations (1992) and his analysis provides the material for the dataset. See S3b for more details. Examples of motifs recorded are shown in Fig. 3 and the distribution of sites is shown in Fig. 4. Taken together, these three cultural forms provide a total of 90 cultural traits collected across around 100 linguistic groups.

Analysis

Phylogenetic analysis. To infer phylogenies we used a character-based method *Mr Bayes* (Huelsenbeck & Ronquist, 2001) that applies Bayesian inference to generate phylogenies based on their likelihood of fitting the observed distribution of trait data. Bayesian phylogenetics provides an efficient way to search for possible trees together with the ability to model different evolutionary scenarios. It has been widely adopted in biological phylogenetics (Huelsenbeck & Ronquist's (2001) paper has over 20,000 citations) and more recently in cultural analysis, such as inference of language family trees (Gray et al., 2009; Bouckaert et al., 2012; Currie et al., 2013), folktales (Tehrani, 2013) and material culture (Matthews et al., 2011). In common with other platforms, *Mr Bayes* employs a Markov Chain Monte Carlo (MCMC) algorithm to perform the tree search (Nunn, 2011: p. 36). This starts with a random tree and set of parameter values (e.g. substitution rates and branch lengths) and randomly modifies them over thousands of iterations. Following an exploratory search of the parameter space ("burnin"), trees are sampled in proportion to their likelihoods, to create a posterior distribution of trees. Because the sampled distribution contains multiple trees it captures and quantifies uncertainty in the phylogenetic relationships among the taxa. For further details of the model used see S4.

Scale of analysis. It is important to analyse the data at a scale at which patterns are sufficiently cohesive and distinctive for phylogenetic reconstruction to be feasible. To do this we use language areas rather than individual linguistic groups. Whilst this approach flattens some of the variations in the dataset it effectively removes the effects of diffusion between close neighbours, thereby improving the visibility of any deeper phylogenetic trends that may be present in the data. Furthermore, as discussed earlier, inconsistencies in ethnographic reporting are likely to have resulted in missing data for individual language groups. Using specifically defined language areas as our unit of analysis helps to ameliorate this problem. Language areas were defined using three criteria. Firstly, that societies within the area were monophyletic in the language tree, i.e. they shared a common ancestor. Secondly, that the number of societies within each was reasonably well-balanced. Thirdly, there were similar numbers of language areas for each cultural type, in order to simplify comparisons between them. Taking account of these criteria, 15 language areas were defined using the Pama-Nyungan phylogeny (Bouckaert et al., 2018). For further details see S1 and S5. To prepare the dataset we recorded traits found in 50% or more of societies as present, and rarer or unknown traits as absent. These criteria was applied to focus on the dominant cultural trait within an area so that, for example, one incidence of trait presence and ten incidences of trait absence would be counted as absent overall (not present overall). Importantly, we are not attributing cultural traits to societies that didn't have them but instead recording those traits in a majority within each area. As some traits did not meet the 50% threshold in any area, this approach resulted in a slighter lower number of traits for the analysis overall (see S5). For mortuary practices, the data is thinly spread across a wide number of societies, therefore trait presence would have been very low using the majority rule. In this case, traits were recorded as present if they were recorded in any of the societies in the language area.

Mr Bayes *results*. Majority-rule consensus trees are illustrated in Fig. 5 (see S4 for more details). Trees were rooted using the

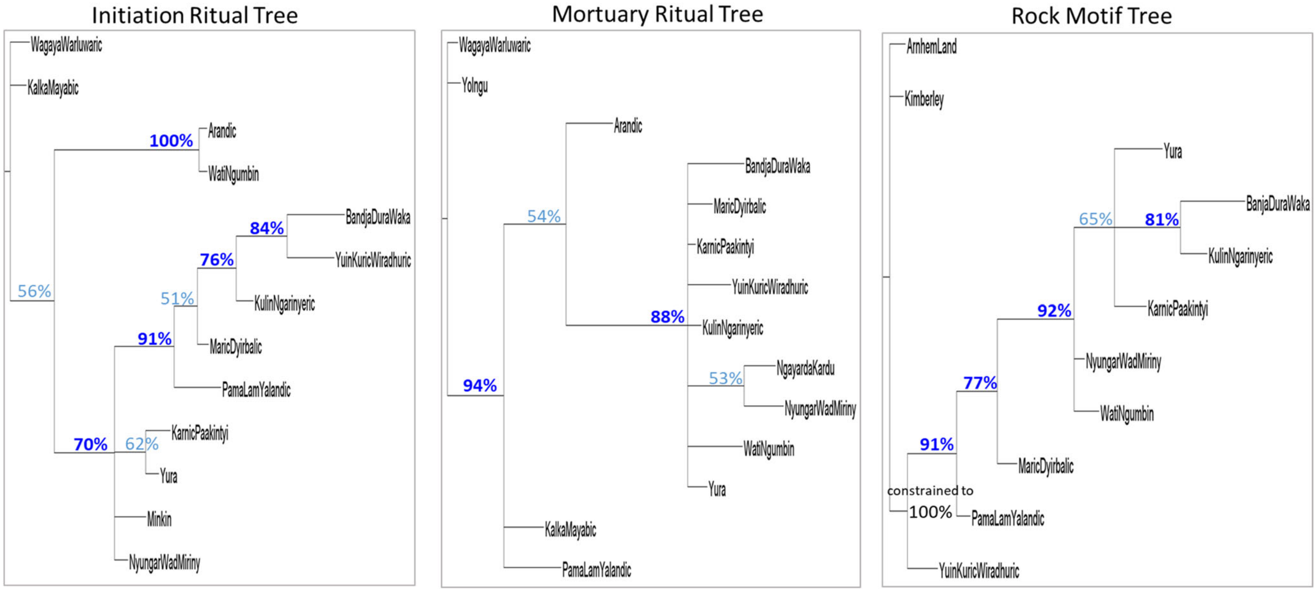


Fig. 5 Majority-Rule Consensus trees (only nodes above 50% posterior support are included) derived from 1501 posterior tree samples generated for each cultural type. Trees shown are phylograms (branch lengths are proportional to the expected number of changes per trait). Nodes ≥50% in light blue, nodes ≥70% in dark blue. All three ritual types had some hierarchical structure and supported nodes. Mortuary was the weakest with only 2 nodes ≥70%, rock motifs had 4 nodes ≥70% and initiation had the strongest support with 5 nodes ≥70%.

conventional assumption that language and culture are closely related (Pagel & Mace, 2004; Gray & Watts, 2017). For initiation and mortuary rituals, *WagayaWarluwaric* was set as an outgroup as it is a likely origin point of Pama-Nyungan language expansion (Bowern & Atkinson, 2012; Bouckaert et al., 2018). For rock motifs, a topology constraint was applied to group all Pama-Nyungan taxa into one clade, effectively setting both Arnhem Land and Kimberley as outgroups. Languages in these regions are hypothesised to have originally shared a common ancestor with Proto-Pama-Nyungan languages (McConvell & Bowern, 2011) so are presumed to be outgroups.

There was support for at least some nodes across all three ritual types but, relative to a 70% level strongly suggestive of phylogenetic fit (Soltis & Soltis, 2003; Alfaro et al., 2003), mortuary had only 2 nodes, rock motifs had 4 and initiation was the most supported with 5. The consensus trees give a strong indication that each ritual type separates into two distinct but different groupings. Initiation has a node with 91% support encompassing eastern regions, mortuary an 88% node grouping southern regions and rock motifs a 92% node including south & west groups. These results suggest initiation and rock motif datasets have a fair degree of phylogenetic structure, with a number of supported nodes, but that mortuary ritual has less. Both initiation and rock motifs also have a well characterised hierarchical structure, with posterior support for sub-groupings deeper in the tree, suggesting these trees may be useful models of trait change. Re-running the analysis without the majority rule criteria used for initiation and rock motifs, i.e. recording overall presence if only one or more traits were recorded, resulted in trees with much less hierarchical structure but with posterior support for similar clades to those discussed above (see S4).

Language comparison. Ritual phylogenies were compared to the Pama-Nyungan language tree to explore the impact of population dispersal on cultural diversity (Mace & Holden, 2005; Riede, 2009; Tehrani et al., 2010). For comparative purposes, phylogenies were aligned to include the nine language areas present across the three ritual trees and the language tree was pruned to these nine regions. Tree comparisons are illustrated in Fig. 6. Rotating taxa to align the tips of the trees (without changing their topology) leads to a close match between language and initiation, but is more 'tangled' in the other two cases. Whilst initiation and language trees are similar, they are not the same. The eastern clade is consistent but the western clade has a different internal structure. This could be driven by the relative homogeneity of Western languages compared to more heterogeneous initiation practices. For example, *WatiNgumbin* initiations have a particularly high number of physical mutilations and this is an isolated taxa in the initiation tree. This language area encompasses the Australian central desert and it is possible that such rites may be a particular adaptation to support the collective action, such as food sharing, necessary for survival in such a precarious environment (Learmouth et al., 2024). There may have also been greater ritual diffusion between some neighbours; *Yura* & *KarnicPaakintyi* are more closely linked in initiation than language. Consensus nodes for initiation had less posterior support in this region (56%, 70% & 62%) than approximate corresponding nodes for language (75% & 98%, from Bouckaert et al., 2018: their Fig. 2). These nodes are highlighted in Fig. 6.

Network analysis. To examine these results further, and provide more confidence in the applicability of a tree-like model, we also analysed the language area dataset using a distance-based network method *Neighbour Net* (Bryant & Moulton, 2004). The aim was to understand the extent to which the data conflict with bifurcating tree models and which taxa are most affected. Networks represent the range of possible relationships between groups graphically, highlighting areas where reconstructed history is conflicted and therefore other influences, such as diffusion between neighbours, may have played a role (Huson & Bryant, 2006). *Neighbour Net* has been used to analyse conflicting signals of inheritance in both biological and cultural systems (Morrison, 2005; Ben Hamed, 2005; Kennedy et al., 2005; Gray et al., 2010; Walker & Ribeiro, 2011; Chen et al., 2013; Tehrani, 2013). The approach assumes that distances between groups, measured as similarities of ritual trait presence, are representative of their

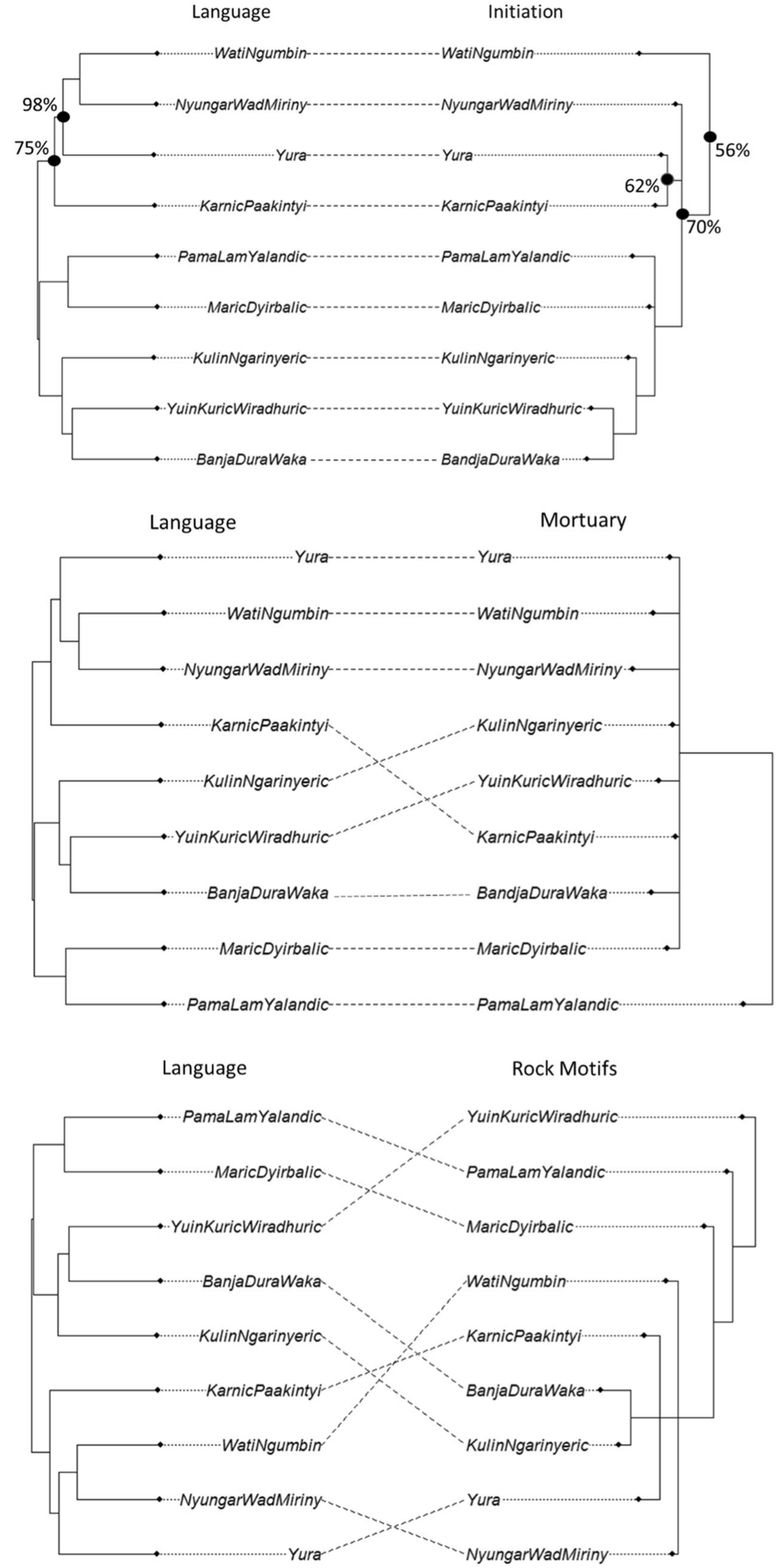


Fig. 6 Tree comparisons using *phylotools* in R (Revell, 2012). Rotating taxa to align the tips suggest alignment between language and initiation but not between language and mortuary ritual or rock motifs. Posterior support values are included for selected nodes in the language vs initiation comparison (discussed in the text).

phylogenetic history. The model generates a distance matrix of trait presence/absence between all possible pairs of taxa and uses a neighbour-joining algorithm to array them in circular space based on the distances between them. The number of parallel lines between taxa, and the length of those lines, provides a visual indication of the level of conflicting signal associated with their network position. To provide a statistical measure of this conflict, a network delta (δ) score can be calculated with 0 indicating the distances between groups exactly fit a bifurcating tree, otherwise, the score is between 0 and 1 (Holland et al., 2002; Gray et al., 2010). δ scores can be compared to other cultural network analyses including languages (Gray et al., 2010) and folktales (Tehrani, 2013). For further details of the *Neighbour Net* model used see S6.

Neighbour Net *results*. The three cultural networks are shown in Fig. 7. Areas that are more boxed or reticulate indicate more conflict in the dataset as to how taxa should be grouped. The network patterns suggest all three datasets have a fair degree of conflict, mortuary ritual the most and rock motifs the least, but all also have some tree-like branching structure. The three networks show some alignment to the geographic locations of language areas, with a number of near-neighbour pairings indicating close cultural similarities that might be expected based on their proximity. In comparison, randomised data would arrange groups equidistantly from each other in no particular order. Lines, or branch lengths, between the taxa give an indication of the distance between them in terms of trait presence and, for all three forms, the networks suggest a division between two groups of taxa. Initiation has an east/west split and mortuary practices are north/south (see the coloured lines in Fig. 7). Both splits are consistent with the Bayesian analysis above.

The rock motif network has the least conflict between regions but is more ambiguous in terms of distinct groupings, in particular, the taxa *MaricDyirbalic* lies between two groups. To investigate further, we examined the neighbour-joining tree derived from the network (this uses the same algorithm as *Neighbour Net* but chooses one node per position to resolve conflicts, see S6). This placed *MaricDyirbalic* closer to the north & east group therefore this split is highlighted in Fig. 7, however, we note that other interpretations are possible. This highlighted split is similar to the results of the analysis conducted by Layton using different distance methods (1992: p. 208). It is also consistent with the Bayesian rock motif tree node which had 92% posterior probability (Fig. 5). There is a clear geographic outlier in the rock motif network with YKW, a south-east region, clustered with taxa located in the north of the continent. The Bayesian tree also positions YKW outside the southern taxa.

Examination of δ scores largely confirms the visual observations of conflict. The rock motif value of 0.23 suggests it has the least conflict and is therefore the most tree-like. Initiation had slightly greater levels of conflict (0.30) and mortuary ritual had the highest level (0.34). Examination of the δ scores by taxa did not indicate any consistently high values, suggesting no particular taxa were associated with higher levels of conflict. Overall, the *Neighbour Net* results are consistent with the Bayesian analysis but suggest slightly more support for a hierarchical tree structure for rock motifs. Summary phylogenetic statistics are shown in Table 2.

Measuring phylogenetic signal. To understand which trait types may have been most subject to cultural descent we used language as the proxy for this and measured their phylogenetic signal relative to the language phylogeny. This also provides a method for validating the first analysis. For example, we would expect the similarity between initiation and language phylogenies prepared from the aggregate area-level data to be reflected in a high phylogenetic signal for these traits at the level of individual linguistic group. The phylogenetic signal was measured using the D statistic designed for discrete or binary traits (Fritz & Purvis, 2010). The model calculates the trait differences between close relatives on the phylogeny (those in sister lineages). When the phylogenetic signal is high, these differences will be small because close relatives will share similar values; in the case of binary traits either all 1's (the trait is present) or all 0's (absent). Subtraction of one value from another will result in only a small difference which approaches zero if the trait distribution exactly mirrors the phylogeny. When the phylogenetic signal is low, sister lineages of the tree will contain traits with different values; for binary traits, a mix of 1's and 0's and therefore the differences between them will tend to be higher. The *D*-value model calculates the average of these sister clade differences for each trait across the phylogeny. Values close to or below 0 indicate the trait has a high phylogenetic signal, whereas those close to or above 1 indicate the signal is low. Values are compared to a null model of trait distribution where $D = 1$ (traits distributed randomly), to assess their statistical significance.

For the analysis, small adjustments were made to the dataset, mainly the removal of societies not included in the Pama-Nyungan phylogeny (see S7). *D*-values were calculated using the *phylo.d* function in R using the consensus language tree (Bouckaert et al., 2018). Observed *D*-values were compared to the null model of random trait distribution ($D = 1$), calculated using 1,000 simulations of randomly shuffled trait values.

Summary results are included in Table 3 (see S7 for individual *D*-values). Compared to the $D = 1$ null model, a statistically significant phylogenetic signal ($p < 0.05$) was demonstrated for 100% (27/27) of initiation traits, 58% (15/26) of mortuary traits, and 24% (9/37) of rock motifs.

For initiation, results support the previous finding of close similarity between initiation and language phylogenies. Traits with the highest signal tend to be associated with genital mutilations, e.g. circumcision, suggesting these practices have been highly conserved during language change. For mortuary rituals, *D*-value results suggest more phylogenetic structure than previously. There is no obvious clustering of trait type; those with statistically significant *D*-values include methods of body disposal, corpse treatment and grave preparation and marking. For rock motifs, only 9 traits (24%) had statistically significant *D*-values, consistent with the previous analysis demonstrating a lack of similarity between rock motifs and language. There was no bias toward particular types; 5 geometric motifs and 4 figurative motifs had significant phylogenetic signals.

Comparison with geography and language. Closely related Pama-Nyungan societies are often spatial neighbours and it is possible that trait clustering may be similar to the phylogeny because of horizontal transmission between societies. Identifying and excluding these traits allows us to better identify those with true phylogenetic signals. To examine geographic relationships, an autologistic model developed by Towner et al. (2012) was used to fit binary traits to phylogenetic and spatial neighbour graphs. Building on the work of Besag (1974 & 1975), the model assumes that trait presence or absence in each society depends probabilistically on its state in that society's spatial and linguistic neighbours. The strength of this dependence is measured by parameters λ (phylogenetic), θ (spatial) and β (a levelling parameter analogous to the intercept in logistic regression). The autologistic model is fitted to each trait by an algorithm that predicts the trait value for each society in turn, determining the most suitable parameters λ, θ and β by combining results from many rounds of prediction. Parameter likelihoods are estimated

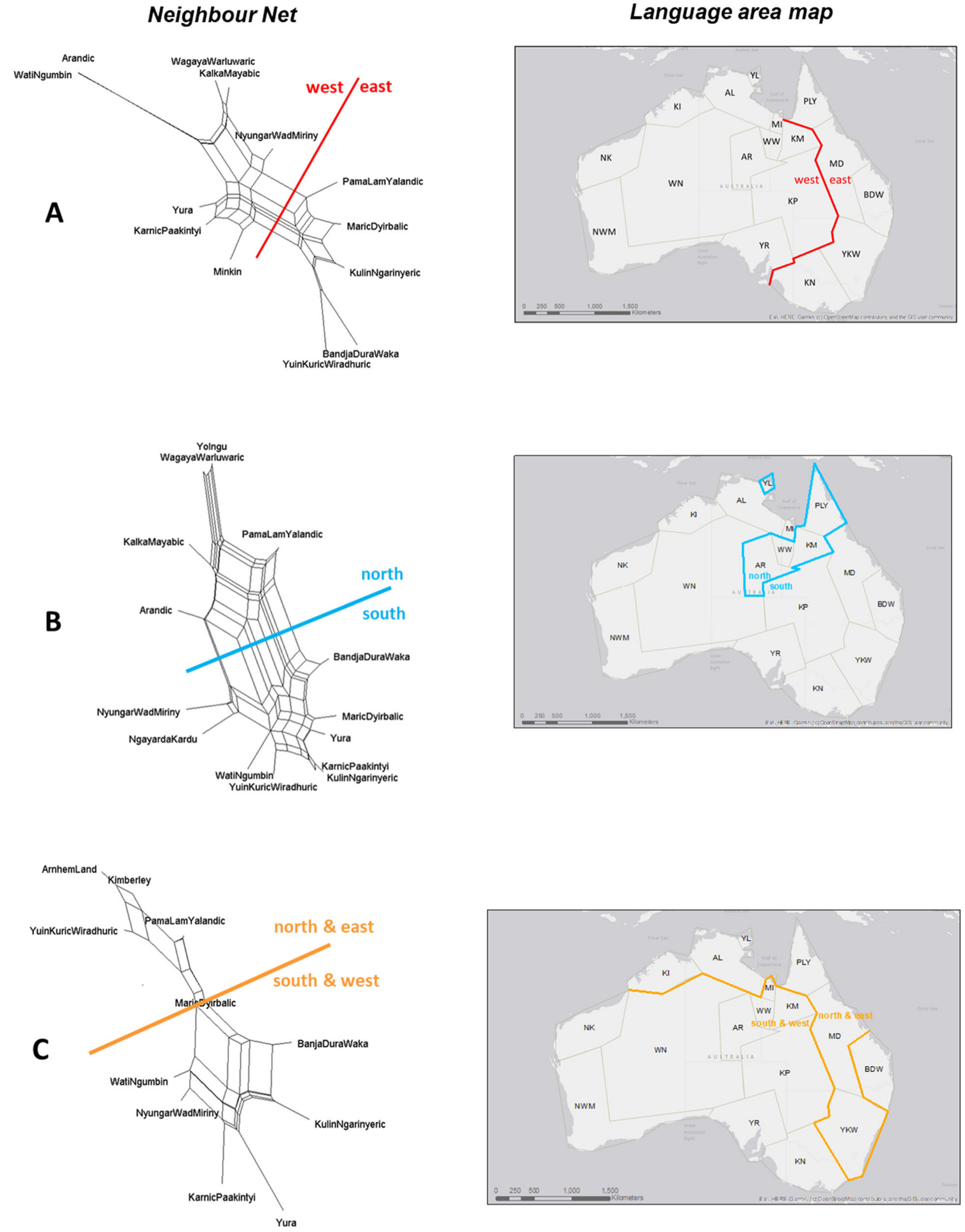


Fig. 7 ***Neighbour Net*** **phylogenetic networks with language area map showing the boundary between divergent cultural traditions. A** initiation ritual, **B** mortuary practice and **C** rock art motifs.

through MCMC simulations using the Gibbs sampler (Geman & Geman, 1984) to generate trait states.

For the analysis, a phylogenetic neighbour graph was constructed based on membership of the same linguistic sub-family, and a spatial neighbour graph was based on distances between location co-ordinates for each society. As data on initiation and mortuary rituals is available for a relatively large number of societies, sub-families (as opposed to the larger

Table 2 Summary of phylogenetic statistics by cultural form.

Method	Phylogeny type	Phylogenetic statistic	Initiation ritual	Mortuary ritual	Rock motifs
Neighbour Net	Distance network	Average δ value	0.30	0.34	0.23
Mr Bayes	Bayesian consensus tree	Number of clades ≥70% support	5	2	4

Table 3 Summary results data for traits analysed in the *D*-value model.

	#societies	#traits	#significant *D* ($p < 0.05$)	% traits significant
Initiation ritual	100	27	27	100%
Mortuary ritual	126	26	15	58%
Rock motifs	47	37	9	24%

language areas used previously) were used to improve model resolution in these cases (see S1). Graphs were calibrated such that societies were connected to similar numbers of spatial and linguistic neighbours. Equalising these distributions ensures both neighbour types are able to have a similar influence on a trait, ensuring their differential effects are reflected in the influencing parameters, θ and λ, rather than being a function of higher relative neighbour numbers (Towner et al., 2012). Metrics for each cultural form are included in Table 4.

To calibrate the graphs, societies were linked with radius distances that enabled the matching of spatial and linguistic neighbours. For example, a 300 km radius for societies with initiation data resulted in 280 spatial and 288 linguistic neighbours. As expected, there was some overlap between the two graphs (spatial neighbours often belong to the same linguistic sub-family). However, all rituals had significant numbers of unique neighbours, enabling the separate effects of proximity and language to be identifiable in the model. For initiation, 75% (210/280) of spatial and 76% (218/288) of linguistic neighbours were unique. Mortuary rituals had 59% unique pairs of both spatial and linguistic neighbours, and rock motifs had 29% unique spatial and 35% unique linguistic neighbours. Using the neighbour graphs, language (λ) and spatial (θ) parameters were estimated for all ritual traits excluding 7 rock art traits that had insufficient frequency (≤ 5) to produce meaningful results. 83 traits were analysed in total. Analysis was in R using Towner et al.'s code. Priors were tuned for parameter values (λ, θ and β, the levelling parameter) for each trait in turn. Final values were estimated using 6000 Gibbs realisations sampled from 12,000 MCMC generations at an interval of two, with the first 600 generations discarded as burn-in.

Results for the 83 traits are included in S7 and the values for λ and θ are illustrated graphically in Fig. 8. Models generally fitted the data well with parameters predicting trait values for societies with an average 78% accuracy. For comparison, Towner et al.'s original paper, which analysed 44 North American Indian cultural traits, had an average predictive accuracy of 83%. The graphs suggest distinct patterns for each ritual type. Initiation trait distribution is strongly influenced by language with minimal influence from geography. Mortuary traits are influenced by both language and geography but only to a limited extent; traits tend to cluster around 0–0.1 for both. Rock motifs have the most scattered distribution with a number of traits showing significant influence from spatial proximity.

Analysis of results at an aggregated level largely supports these observations. Mean values of positive and negative parameters were calculated for each ritual type (Table 5). Positive values indicate traits are more likely to be present in society if they are also present in neighbouring societies. Negative values indicate traits are more likely to be present if they are *absent* in neighbours. Initiation has the strongest overall influence from phylogenetic (linguistic) neighbours (0.20) and a relatively low influence from geography (0.04), suggesting a close association to language, even when proximity is considered a potentially confounding factor. Mortuary rituals had low values for phylogenetic and spatial proximity (and the highest for the balancing β parameter), suggesting other factors have impacted trait distribution. This conclusion fits with the weaker phylogenetic structure observed earlier, reinforcing the idea that mortuary ritual traits are quite labile. Different practices may have been widely adopted across societies, with variation observed in the ethnography perhaps more influenced by the social status of the deceased than by inherited tradition. Rock motifs were the most influenced by spatial neighbours ($+0.10$) suggesting relatively high levels of diffusion. Rock motifs also had the highest negative values (-0.23 and -0.08) among ritual types, suggesting neighbour presence is more likely to result in trait absence (see below).

Individual traits were assessed in comparison to the *D*-value results to determine which had confirmed phylogenetic signal, i.e. that the positive signal was not due to geographic proximity. If trait presence depended more strongly on the effect of λ (linguistic neighbour) than of θ (spatial neighbour) we considered this evidence of confirmed phylogenetic signal. 51 traits had statistically significant *D*-values and of these 41 (80%) also had positive evidence of phylogenetic influence in the autologistic analysis (traits highlighted in Table 1). For comparison, an analysis of Indo-European folktales using the Towner et al. autologistic model and the same *D*-value criteria found 76% of tales were more strongly influenced by their linguistic rather than spatial neighbours (Da Silva & Tehrani, 2016).

Of these 41 traits, 26 relate to initiation (out of 27 with significant *D*-values). As in the *D*-value results, traits with the highest linguistic signal were associated with genital mutilations, e.g. female genital mutilation ($+0.45$), circumcision ($+0.36$), sub-incision ($+0.35$). These results confirm that such practices have been highly conserved with language change, with little influence from geographic proximity, suggesting they are important signifiers of group identity. In only one case did λ not exceed θ; male tooth extraction. Here, the spatial effect ($\theta = 0.14$) was equivalent to linguistic ($\lambda = 0.14$) suggesting a prominent role for diffusion. Nine mortuary traits (out of 15 with significant *D*-values) had confirmed phylogenetic signal ($\lambda > \theta$); 3 were related to compound disposal suggesting these more complex practices may have been inherited with Pama-Nyungan dispersal. Six rock motifs (out of 9 with significant *D*-values) had confirmed signals, of these only 2 were geometric (*mazeForms* and *humanFootprints*) which provides little support for the association between this design and Pama-Nyungan dispersal.

In addition to the 41 traits with confirmed phylogenetic signals, an additional 23 traits had evidence of greater linguistic than spatial influence ($\lambda > \theta$): 8 mortuary traits and 15 rock motifs. The effects on mortuary trait distribution were small (less than 0.1 in most cases). The results for rock motifs bear closer scrutiny, however. Four traits had a relatively high linguistic contribution (0.16 to 0.25) that was combined with a negative spatial effect (−0.08 to −0.22). Such results suggest distribution of these traits (*dots, tridents, lizardHumanForms* and *mazeForms*) follows a pattern of linguistic inheritance but where geographical proximity is more likely to result in trait absence. Potentially, such traits could act as unique identifiers, perhaps acting as markers of shared group identity within a particular territorial area. In addition, two traits also had negative values for linguistic influence: *snakeForms* (−0.19) and a very high value for *arcs* (−0.85) which was an outlier in the dataset. Such traits could also be acting as markers but in this case to delineate *between* closely related societies.

In general, proximity seems to play a more important role in rock motif distribution than mortuary or initiation distribution. Four traits had relatively high results for positive spatial influence (+0.16 to +0.29): *concentricCircles, macropodFootprints, barredCircles and stemmedCircles*. Such designs commonly represent 'birds-eye' views of marks left on the sand by animals, humans or ancestral beings (Layton, 1992: p. 148). In central Australia, they are frequently combined to depict journeys by Dreamtime beings that may coincide with optimal walking tracks between water holes or foraging routes (*ibid*, 55, 72 & see Fig. 9). For example, the concentric circles used by the *Warlbiri* may signify either campsites or the tracks of totemic species (Munn, 1973). That such walking or dreaming tracks are often shared between societies may explain why, in this analysis, the effect of spatial neighbours is greater than linguistic neighbours for these motifs.

Table 4 Neighbour graph metrics.

	Initiation	Mortuary	Rock motif
Number of societies	100	143	49
Language sub-families	20	22	12
Spatial radius (km)	300	350	450
Spatial neighbours:			
Total	280	555	103
Average per society	*5.6*	*7.8*	*4.2*
Unique	210	327	30
Linguistic neighbours:			
Total	288	557	111
Average per society	*5.8*	*7.8*	*4.5*
Unique	218	329	39

Discussion

Our ability to infer partial phylogenies for initiation rituals and rock art suggests these forms have maintained sufficient coherence over time for their history to be at least partly recoverable. In contrast, our reduced ability to do this for mortuary rituals suggests these practices have had limited coherence over time. Our results also indicated a consistently strong association between the phylogenetic history of initiation ritual and that of language, which was consistent across all the analytical approaches. This link to language was much weaker for rock art and mortuary practice; at the holistic level there was little association, but at the individual trait level some traits did have a phylogenetic signal (after adjusting for the impact of geography): 35% of mortuary traits and 16% of rock art motifs.

A useful framework for thinking about cultural coherence was first developed by Boyd et al., 2005 (later discussed in Gray et al., 2007; Riede, 2009; Tehrani et al., 2010). Boyd et al. hypothesised that cultures, defined as systems of socially transmitted information, could be classified into types depending on the extent to which cultural descent and diffusion contributed to their evolution. They grouped these along a continuum of decreasing levels of phylogenetic stability:

1. All the elements that make up a culture cohere and resist recombination, therefore phylogenies are relatively easy to infer.

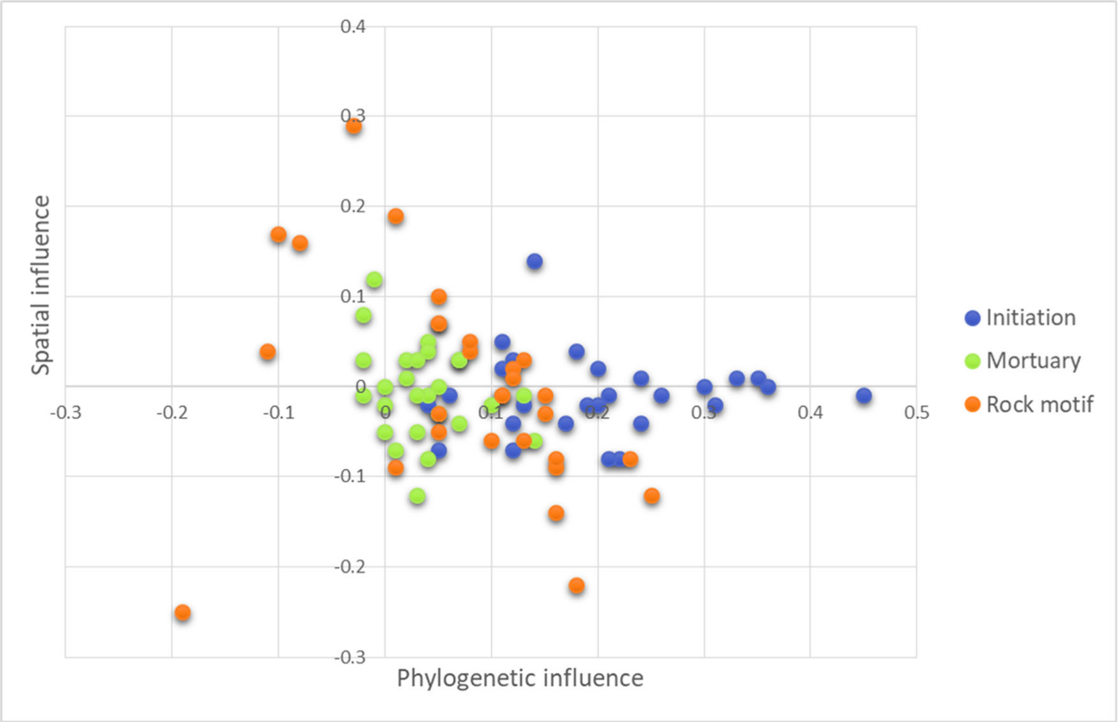


Fig. 8 Autologistic modelling of traits by ritual type. Axes represent the level of dependence on trait distribution from phylogenetic (linguistic) neighbours (horizontal axis), and from spatial neighbours (vertical axis). One outlying data point not plotted for rock motifs: arcs λ −0.85, θ −0.05 (see text).

Table 5 Autologistic results by ritual type.

	+phylo (λ)	−phylo (λ)	+geog (θ)	−geog (θ)	($-\beta$)
Initiation	0.20	0.00	0.04	0.03	0.24
Mortuary	0.05	0.02	0.04	0.04	0.65
Rock motifs	0.11	0.23	0.10	0.08	0.09

2. A conservative *core tradition* in each culture is identifiable that is rarely affected by diffusion from other groups. However, peripheral elements may be heavily subject to cross-cultural borrowing. Phylogenetic reconstruction requires distinguishing between core and peripheral traits.
3. Cultures are best represented as *packages* of smaller elements. Each package is relatively unaffected by recombination but has its own history of inheritance. Reconstruction requires the identification of stable cultural domains and their separate phylogenies.
4. There are no observable entities of culture that are sufficiently coherent, or stable over time, for phylogenetic reconstruction to be useful.

Viewing our results in these terms, would suggest Pama-Nyungan culture, as delineated here, is not maximally coherent (type 1) since cultural forms do not have similar histories or variations. Initiation ritual, however, because it is reconstructed in a similar way to language (which we take as our proxy for cultural descent), could be described as a *core tradition* (type 2) in Boyd et al. terms. Rock motifs, with their own history of inheritance, unrelated to language, might best be described as type 3. Phylogenetic methods were unable to reconstruct a clear descent history for mortuary ritual but there was support for some deeper nodes that suggest type 3/4 is probably the best description.

The identification of initiation as a core tradition indicates a relatively high level of coherence rarely affected by diffusion from other groups. Intuitively this makes sense as initiation is closely tied to group membership which in turn is closely tied to the language the group speaks. As discussed in the Introduction, ethnographers have noted the transmission of ceremonial complexes and other ritual elements between societies, e.g. mythical narrative cycles, rock art imagery, decorative items (Layton, 2003; Gray, 1978; Elkin, 1952; Haynie et al., 2014) but perhaps more stability in the ritual practices themselves. Elkin (1961: p. 202, quoting Robertson Smith (1927: p. 18)) compared the relatively high variability of mythical narratives between societies to those of ritual practices, which tended to be more similar, i.e. more stable over time. Similarly, Meggitt (1966: p. 197) noted the myth cycle adopted by the Warlbiri, which originated in the north-west, a long distance from their homeland, was not linked to the ritual practice of sub-incision which already featured in their pre-existing narratives. Thus our results tend to support this latter perspective and illustrate, in more general terms, how a quantitative approach may provide further insights into cultural transmission, revealing trends not always visible in more 'close-up' ethnographic research.

The close association between initiation and language lends support to the idea, as suggested by some authors, that the development of complex initiation practices might have played a role in the expansion of the Pama-Nyungan language family throughout the Australian continent. As discussed earlier, Evans & McConvell (1998) suggested the adoption of a more 'open culture of outward-reaching social alliances' could have been the driving force behind the expansion, achieved through a combination of new kinship systems and the introduction of large-scale ceremonial activity orientated around novice initiations. However, while our results support the idea of initiation as a core cultural tradition, they do not prove it was a stimulus for Pama-Nyungan expansion. Such traits could simply be neutral, passed along with language change, without conferring any particular benefit. A positive demonstration of this effect would require a different analysis, possibly one connected with analysing the effect of traits on the diversification of the language phylogeny (e.g. Maddison et al., 2007).

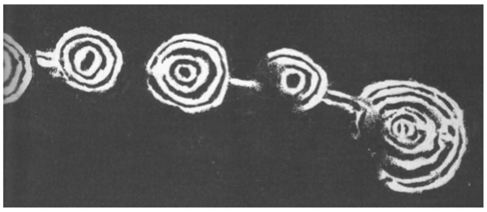


Fig. 9 Concentric circle rock motifs. The circles are linked by lines to depict the journey of the *K.* pythons to Mutitjulu, Uluru (Layton, 1992: p. 53).

Turning to mortuary rituals, the limited support for phylogenetic reconstruction suggests these practices may be quite labile, with a mix of rituals used in a region that depends, for example, on the social status of the deceased. However, our results do provide some support for a generalised north/south divergence in mortuary traditions (Fig. 7) that warrants further examination. Relatively complex compound disposals (initial rites followed by a much later disposal ceremony) are also practiced in South East Asia, including parts of Indonesia, and some authors have suggested the tradition diffused from there to Australia (Elkin quoted in Berndt & Berndt, 1996: p. 460; Arthur & Morphy, 2005: p. 98; Meehan, 1971: p. 281). To examine this idea more closely, we analysed the distribution of compound disposal practices (Fig. 10) but did not find any support for a north/south axis across all forms of compound disposal, although distribution where burial is the first step had a slight northern bias. Looking at the individual trait analysis (Table 1), three traits with significant phylogenetic signals were associated with compound disposal (including the burial form) which suggests a distribution more closely associated with language change than diffusion. We therefore find little support for the theory that compound disposal diffused through Australia after first arriving from countries in the north.

The confirmed phylogenetic signal found in 9 mortuary traits suggests that, as with initiation, they could be associated with Pama-Nyungan expansion. Mortuary practices have not been specifically linked to this process in the literature but their features, such as complex rites, enactments and large-scale gatherings, suggest they may be relevant. Mythical narratives, including those linked to the later rites associated with compound disposal, are frequently associated with guiding the deceased spirit to their clan estate, which could be interpreted as maintaining the continued attachment of clans to the territory (Peterson, 1972). Such rites could plausibly be related to the development of clan totemism, and the changes in kinship and ritual obligations hypothesised to be associated with Pama-Nyungan expansion

The analysis of rock motif diversity suggests it is best represented as a type 3 process with its own history of inheritance, separate from the core cultural elements of language and initiation. Consequently, we don't find support for the association of rock motif change, such as the expansion of geometric motifs, with Pama-Nyungan language expansion. If this were the case, we

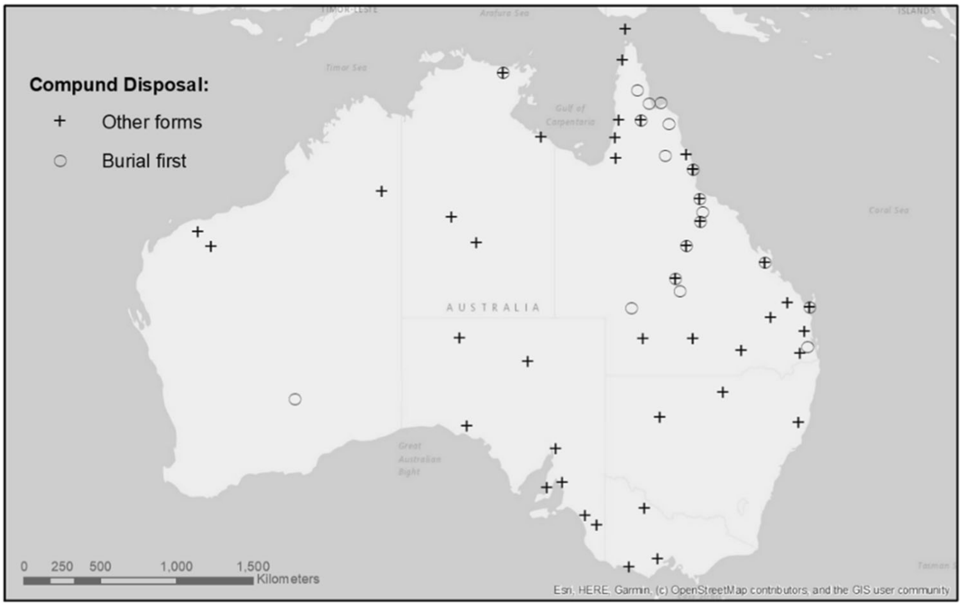


Fig. 10 Distribution of societies with compound disposal mortuary rites. Those where burial is the first step and those where other forms are the first step (either drying, elevation, retention or cannibalism) are indicated on the map.

might have expected a close relationship between the rock art phylogeny and that of language. We also don't see any particular link between geometric motifs and language. In the individual trait analysis, only 6 out of 37 motifs (16%) had confirmed phylogenetic signals (Table 1) and only 2 of these were geometric.

Why might rock motifs have an independent history? Although they cannot be demonstrably linked to language change, at least some of their phylogenetic structure is identifiable. It is not clear what processes may have shaped motif development but overland exchange networks have been documented by a number of authors (McCarthy, 1939; Peterson, 1976; McBryde, 1984) and a central north/south axis appears to have been frequently (though not universally) used as a conduit for items such as axe heads, red ochre, pituri ('native tobacco') and decorative shells. Our analysis suggests a similar axis of orientation (north & east vs. south & west, Fig. 7) and it is plausible that novel rock motifs may have been transmitted along this route using pathways perhaps more aligned to exchange than to language expansion.

In conclusion, our results suggest, firstly, that existing ethnographic material can be usefully assembled to create new cultural datasets that facilitate the use of computational methods. Secondly, careful deployment of a combination of methods enables us to accommodate the effects of both vertical and horizontal modes of inheritance. This is a dynamic field and a recently published model that combines both modes of transmission within a Bayesian framework maybe applicable for such analyses in the future (Neureiter et al., 2022). Thirdly, a comparison between cultural types can illustrate how culture is not homogenous, with different forms exposed to different forces of change within the same group of societies. Furthermore, if a cultural form can be categorised as a core tradition, as is the case here with initiation, it may indicate a particular prominence in the history of a society that would benefit from further investigation. Lastly, our results suggest a quantitative approach to cultural diversity can usefully complement existing scholarship and enable theories to be tested in a robust and principled way.

Data availability

Supporting data is available in the Supplementary Information.

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The authors declare no competing interests.

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Correspondence and requests for materials should be addressed to Duncan Learmouth.

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