

Phylogenetic reconstruction of Bantu kinship challenges Main Sequence Theory of human social evolution

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Kinship provides the fundamental structure of human society: descent determines the inheritance pattern between generations, whereas residence rules govern the location a couple moves to after they marry. In turn, descent and residence patterns determine other key relationships such as alliance, trade, and marriage partners. Hunter-gatherer kinship patterns are viewed as flexible, whereas agricultural societies are thought to have developed much more stable kinship patterns as they expanded during the Holocene. Among the Bantu farmers of sub-Saharan Africa, the ancestral kinship patterns present at the beginning of the expansion are hotly contested, with some arguing for matrilineal and matrilocal patterns, whereas others maintain that any kind of lineality or sex-biased dispersal only emerged much later. Here, we use Bayesian phylogenetic methods to uncover the history of Bantu kinship patterns and trace the interplay between descent and residence systems. The results suggest a number of switches in both descent and residence patterns as Bantu farming spread, but that the first Bantu populations were patrilocal with patrilineal descent. Across the phylogeny, a change in descent triggered a switch away from patrifocal kinship, whereas a change in residence triggered a switch back from matrifocal kinship. These results challenge “Main Sequence Theory,” which maintains that changes in residence rules precede change in other social structures. We also indicate the trajectory of kinship change, shedding new light on how this fundamental structure of society developed as farming spread across the globe during the Neolithic.

kinship | Bantu | phylogenetics | Bayesian | Neolithic

Kinship is the key structure underlying human society: descent determines how wealth, land, and position are inherited across generations, whereas residence describes the rules governing where a couple should move to once they are married (1). In turn, descent and residence patterns determine other key relationships within society such as alliance, trade, and marriage partners (2). Contemporary hunter-gatherer societies, which are often considered a model for preagricultural human societies, are predominantly bilateral, tracing descent through both lines, and multilocal, with each couple choosing where to live (2–4, but see ref. 5), allowing for flexibility in those societies. In the last 10,000 years, however, a number of groups developed agriculture, which led to the expansion of food production techniques, cultures, and in some cases their populations too (6). The emergence of farming is thought to have coincided with more sex-biased dispersal and unilineal kinship (7).

From their ancestral homeland in the Benue valley in Eastern Nigeria 3,000–5,000 BP (8, 9), possibly using a grassland corridor that opened up through the Cameroon rainforest (10, 11), the Bantu undertook one of the great farming expansions of the Neolithic (6). The history of their kinship is therefore key to debates about the fundamental processes that drove the evolution of human society during the Holocene. However, there are

disagreements about the ancestral pattern of Bantu kinship and how this evolved through time.

Vansina (12) suggests that proto-Bantu society had a bilateral descent and bilocal residence system (definitions in *SI Appendix, Table S1*) that was adaptive for expanding populations. Based on linguistic reconstruction, such as the proto-Bantu word for “house” being sex neutral, he argues that residence was flexible (13). Hunting required cooperation and mobility, and would be best served by males having a choice about their residence rather than being constrained by unilocality (12). Vansina suggests that only in the 18th or 19th century did unilineal descent and residence patterns begin to emerge, due to increased wealth and the disorder faced by some Bantu-speaking people (12).

The second theory proposes a unilineal descent and unilocal residence system in the ancestral Bantu population (14). Hage and Marck argue, based on the linguistic reconstruction of kin terms, that the early Bantu speakers were, in fact, matrilocal and matrilineal (see also ref. 3), and dispute the sex neutrality of the proto-word for “house.” They also suggest that matriliney is consistent with a people that face an external threat experienced as populations expand and colonize new territory, arguing that absent males would trust their sisters, but not their wives, to look after their common lineage interests (15). Crucially, Marck and Bostoen (7) argue that matrifocal Bantu cultures dissolved with residence changing first from matrilocal to patrilocal, thus supporting Divale’s (16) proposal that changes in residence drive changes in inheritance patterns for a migrating population. This

Significance

The agricultural revolution had a dramatic effect on all aspects of human society, but piecing together how humans lived as they spread farming practices worldwide remains difficult. In particular, the fundamental structures of human society, namely the way that property is inherited and the rules governing post-marriage residence, do not leave a clear trace in the archaeological record and, therefore, have been largely intractable. However, the recent availability of phylogenetic language trees coupled with new Bayesian statistical techniques makes it possible to reconstruct the ancestral state of Bantu kinship and reveals that inheritance and residence rules coevolved as farming spread throughout sub-Saharan Africa. Our results question current theory suggesting that residence rules are the primary driver of all other human social structures.

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suggestion provides support for “Main Sequence Theory,” which proposes that worldwide there is a pattern of change with residence rules driving change in other social structures (2). In particular, Murdock argues “when any social system undergoes change, such change regularly begins with a modification in the rule of residence” (ref. 2, p. 221). Changes in descent follow and are always consistent with the change in residence. Changes in kinship terminology are affected by changes in both residence and descent and may follow some considerable time afterward (2).

There is therefore no agreement among researchers about the ancestral states or patterns of change in kinship traits among Bantu societies based on historical linguistic methods. There are a number of problems with relying solely on reconstructions of ancestral vocabulary to infer social organization in the past. First, although linguists use systematic methods of reconstructing proto-forms based on regular sound changes (13, 14), there is still an element of subjectivity in this approach, which can lead different researchers to suggest contradictory results based on the same words (7, 13, 14). Furthermore, the inference of social organization in a past society is a further step removed from this process and assumes a direct relationship between particular words and particular forms of organization. Although it may be possible to reconstruct the sound of a particular lexical item, the meaning of such a word is less clear because of the possibility of semantic shifts (17).

Phylogenetic comparative methods, adapted from evolutionary biology, offer an alternative way of reconstructing the evolutionary history of cultural traits such as kinship structures. These techniques map the traits of interest (in this case descent and residence) onto a phylogenetic tree, which represents the way societies are related to each other historically. The likely forms of these traits in past societies can then be inferred by using an explicit statistical model of trait evolution. Importantly, these reconstructions are probabilistic, meaning it is possible to assess how much confidence to place in any particular reconstruction. The likelihood of alternative hypotheses for the pattern of evolution of traits over the tree can then be estimated. Furthermore, performing analyses over a sample of phylogenetic trees can explicitly incorporate uncertainty about the historical relationships between societies. These methods can be used to estimate the cultural history of a language family, even where historical records or archaeological evidence are absent, and have been used to examine the history of residence patterns in both the Indo-European and Austronesian language families (18, 19).

The Bantu speaking people of sub-Saharan Africa represent one of the major early farming expansions; the advantage of agricultural food production allowed a single language group to displace and expand into the lands of previous hunter-gatherer populations (6). This process has allowed for language phylogenies of Bantu societies to be generated (9, 20–22), which can be combined with comprehensive data on extant kinship patterns across a large number of Bantu cultures (23, 24) to infer historical patterns of cultural evolutionary change. A previous attempt to infer the ancestral state of descent for the original Bantu population (25, 26) was inconclusive, possibly because of the small sample size, the single phylogeny (20), or the maximum likelihood methods used.

Here, we advance previous attempts to reconstruct the kinship traits across the Bantu language family by applying Bayesian phylogenetic comparative methods (27–29) to a dataset of 122 Bantu ethnolinguistic groups to infer the ancestral state and evolutionary trajectory of Bantu kinship patterns. Analysis of basic vocabulary items (30) has enabled the phylogenetic relationships among more than 500 Bantu languages to be inferred (9), which has increased the scope for the number of different Bantu cultures that can be analyzed and enabled the incorporation of groups that were underrepresented in previous analyses. In particular, the current sample includes a number of

additional societies from the “Northwest” and “Forest West” regions, which may be particularly important in inferring trait states at the earliest nodes in the trees. Furthermore, Bayesian phylogenetic methods, which can incorporate uncertainty about the phylogenetic relationships between cultures, provide a more accurate picture of the inferences that can be drawn from comparative data. In this way, it is possible to infer the ancestral states of kinship traits and, hence, reconstruct the cultural history of the Bantu expansion, which means it is possible to estimate the likely order of trait change and test whether changes in residence rules precede changes in inheritance patterns as proposed by Main Sequence Theory (2, 7, 16).

Results

We found both descent and residence patterns showed strong phylogenetic signal among Bantu-speaking cultures. A *phylo.d* test (31) revealed that both traits have phylogenetic patterning that is extremely unlikely to occur by chance ($P < 0.001$) and are not significantly different from Brownian motion (*SI Appendix, Table S2*), which supports models in which descent and residence patterns each evolve along the branches of the Bantu language tree.

We inferred the ancestral states for kinship traits at the root of the Bantu language tree by using a reversible jump (RJ) Markov chain Monte Carlo (MCMC) method, which simultaneously explores the posterior sample of phylogenetic trees and possible models of evolution of traits on the tree, visiting models in proportion to their posterior probability (32). This method allows for uncertainty in the phylogeny and the stochastic nature of the evolutionary process. We find strong support ($P = 0.995$) for patrilineal descent at the root of the phylogeny, whereas for residence, there was a high probability ($P = 0.999$) that the root was patrilocal (*SI Appendix, Table S3*).

A previous study (25) was unable to resolve the ancestral state for descent, but showed that the adoption of cattle herding led to switches to patriliney. It might be argued that the Bantu adoption of cattle in East Africa from their Cushite neighbors (33, 34), during the Bantu expansion, could falsely suggest a patrilineal root. To check for this false result, we performed a correlated evolution analysis of descent and cattle herding in the *Discrete* package in *BayesTraits* (27). Both the independent analysis, where the traits are forced to evolve separately, and the dependent analysis, where they can evolve together, showed strong support for patriliney without cattle herding as the ancestral Bantu state, indicating that the later adoption of cattle did not falsely influence the root reconstruction for descent.

The reconstruction (Fig. 1) of the probability of states at ancestral nodes across the phylogeny suggests that from patriliney as the descent pattern at the root (A) of the Bantu phylogeny, there was an initial switch to matriliney (B) in a few Forest West Bantu cultures (following ref. 35) and those in the West Savannah. As Bantu populations spread further across into East Africa and then South, there was a subsequent shift back to patriliney (D), followed by a switch to matriliney (E) in the South East Bantu and then a shift to mixed descent (F) and a final change back to patriliney (G) as Bantu populations reached the southern tip of Africa (Fig. 1). Residence followed a similar pattern to descent, except that there was a secondary switch back to patrilocal at (C) instead of (D), and the final switch to patrilocal came at (F) not (G) (*SI Appendix, Fig. S4*). Neolocality is shown to be a recent phenomenon supporting earlier research (36). The pattern for both descent and residence is so similar as to suggest correlated evolution between these two traits as Bantu-speaking populations spread across sub-Saharan Africa.

To test for correlated evolution between descent and residence and assess whether changes in residence were driving changes in descent, as proposed by Main Sequence Theory (2), the RJ procedure in the *Discrete* package in *BayesTraits* (27) was

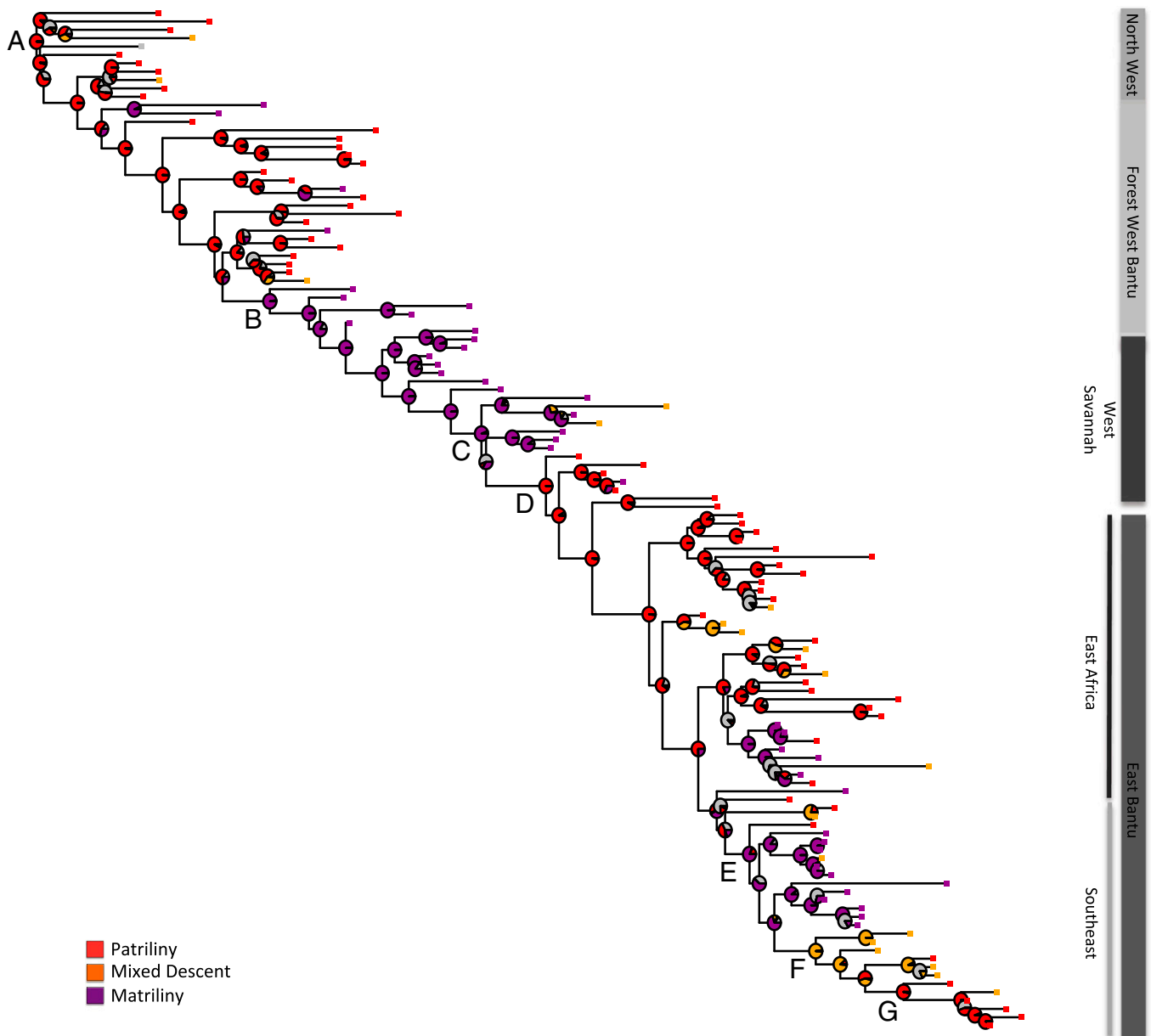


Fig. 1. Ancestral reconstruction of descent across Bantu cultures. The pies at each node show the mean probability of each state from the MCMC analysis plotted on the consensus tree. Gray in the pies shows uncertainty that the node exists in the tree sample. Letters (A–G) denote switch points in the state of descent along the expansion route on the phylogeny, for comparison with the residence trait (*SI Appendix, Fig. S4*). Cultural groups follow Guthrie (32).

used. A \log_{10} Bayes factor of 3.11 suggests decisive support for correlated evolution between descent and residence across the Bantu phylogeny (*SI Appendix, Table S4*).

Fig. 2 shows the reversible-jump analysis of correlated evolution between the traits. There are two routes from the ancestral state of patriliney and patrilocality to the derived state of matri/bilateral descent and matri/neolocal residence: the one in which descent changes first (transitions q_{13} and q_{34} via state C) and the one where residence changes first (q_{12} and q_{24} via state B) (*SI Appendix, Fig. S9*). In the reversible jump analysis, the route where descent changes first (transitions q_{13} and q_{34} , via intermediate state C) is more likely, with both transitions assigned to zero in none or a very small proportion of the posterior distribution. This result suggests that, for changes from the ancestral state to the derived state, descent changed first, and therefore, because the traits show correlated evolution, probably

drove changes in residence. However, there were a number of switches between states in both descent and residence, and for the transitions in the other direction (i.e., from matriliney/matrilocal to patriliney/patrilocality), residence changed first. To check these findings, likelihood comparisons were made between models where the transition rates of the two routes between patriliney and matriliney cultures (via state B or state C in Fig. 2) were each forced to zero. The transitions via state C were shown to be decisively more likely, providing strong evidence to support the reversible-jump analysis (*SI Appendix, Tables S5 and S6*), which suggests that changes in descent drove shifts away from patriliney cultures, whereas residence drove reversals from matriliney back to patriliney cultures. In other words, in moves between patriliney (A) and matriliney (D) cultural states, an intermediate state of matriliney with patrilocality (C) is much more likely than an intermediate state of patriliney with matrilocality

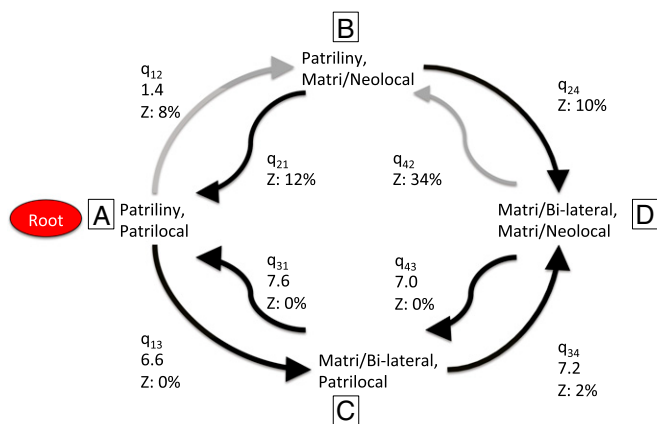


Fig. 2. Estimated rate parameters of correlated evolution between descent and residence across the Bantu phylogeny under the RJ MCMC analysis. Z denotes number of times the transition rate is assigned to zero as a proportion of posterior probability distribution. Thickness of arrows reflects proportion of time transition rate is not assigned to zero. Number below rate name (q_{ij}) is the mean transition rate where rate distribution approximates normal. Gray line denotes a slow transition rate. Letters next to states denote root (A), derived state (D), and intermediate states (B and C).

(B) (Fig. 2). This transition may occur because the combination of patrilineal inheritance and matrilineal residence is a very unstable or unusual state, at least in Africa; an intermediate state of patrilineal residence combined with matrilineal or other forms of inheritance may be a more common intermediate state, from whatever ancestral condition it derives.

Discussion

Our results show that even when archaeological and historical evidence are lacking, it is possible to go beyond historical linguistic inference, which is highly contested in the Bantu case (7, 12–14), and reconstruct the ancestral states of kinship traits throughout the Bantu expansion. Our analyses, based on the most comprehensive Bantu language phylogeny available (9), suggest that the ancestral Bantu society, which was located in the Benue Valley on what is now the Nigerian/Cameroon border, was both patrilineal and patrilocal. As far as residence is concerned, this result is consistent with genetic studies on sub-Saharan farmers that are argued to imply a patrilocal history; fast evolving polymorphisms indicate that the ratio of mtDNA to Y-chromosome variation is much higher in farming than hunter-gatherer populations, suggesting females moved residence before they reproduced, whereas males stayed in their natal locality (37–39).

The results of this study do not support the conclusions of either of the historical linguistic studies of the Bantu (7, 12–14). Instead of the bilateral and ambilateral kinship proposed by Vansina (12), or the matrilineal and matrilineal kinship proposed by Marck and coworkers (7, 14), our analyses support yet another hypothesis, providing evidence for the first time to our knowledge that the kinship pattern for the ancestral Bantu population was both patrilineal and patrilocal. Furthermore, the phylogenetic methods used enable us to postulate that for both traits, there were switches back and forth between patri-focal and matri-focal states as the Bantu populations expanded throughout sub-Saharan Africa. These switches suggest that there was some flexibility in these traits as Bantu populations spread southwest, but that unilineal descent systems were retained throughout Bantu history, in contrast to the scenario proposed by Vansina (13).

Despite being unable to resolve the ancestral state of descent among the Bantu, Holden and Mace (25, 26) were able to suggest that patriliney is associated with pastoralism. Matriliney could

emerge because of the loss of cattle, tsetse fly infestation (26), or some other cause (40), which may have reduced the pressure for inheritance through the male line. The results presented here suggest that, in turn, changes in descent may have driven residence patterns to change to matrilineal.

Overall the phylogenetic comparative approach taken here to infer social organization in past societies offers improvement over relying completely on historical linguistic reconstructions. In particular, this approach allows direct inference of the ancestral states of the particular traits of interest, rather than tackling the issue obliquely via kinship terminology. It would be interesting to reconstruct kinship terminology explicitly using phylogenetic comparative methods to examine the relationship with direct estimates of social organization and as a point of comparison with traditional methods. Archaeological information could also potentially be of use in inferring kinship structures in past human societies. Although many aspects of social organization do not leave direct material remains in the archaeological record, it may be possible to make plausible inferences based on, for example, mortuary practices (41, 42). Unfortunately, the current archaeological record in Africa is incomplete because of the environmental conditions in the equatorial rainforest, which are particularly problematic for the preservation of the remains of human societies of the past (33). However, the results reported here do at least provide predictions about the likely forms of social organization in past societies that could in theory be tested as archaeological data accumulate.

Our results clearly demonstrate that both residence and descent, which are the key aspects of kinship, coevolved as Bantu populations moved through sub-Saharan Africa. As well as identifying correlated evolution between these traits, the model of evolution indicates that descent changed first for moves away from patrilineal states, whereas residence changed first for moves back from matrilineal states. When inheritance through the male line breaks down, so that wealth is no longer passed from father to son, women may be more likely to stay with their relatives, postmarriage, to garner support from close relatives in tasks such as child rearing. Indeed, communal breeding by related females has been shown to promote matrilineality (43). That descent could change before residence questions Main Sequence Theory, which proposes that it is changes in residence rules that drive changes in the whole social structure of a society (2, 16). In the Bantu at least, our results suggest that residence only drives changes away from a matrilineal pattern, which may indicate that the costs and benefits of changing kinship patterns differ depending on whether the culture is patrilineal or matrilineal.

Methods

Data. Ethnographic data were derived from the Ethnographic Atlas (23, 24) and matched to the language data by name and geographic location (following ref. 19).

For the descent pattern variable 43 of the Ethnographic Atlas (23, 24), descent: major type, was used. Among Bantu-speaking populations the six states featured are as follows: 1, patrilineal; 2, duolateral; 3, matrilineal; 4, quasi-lineages; 5, ambilineal; 6, mixed (*SI Appendix, Table S1*). For ancestral state analyses, the three states used were as follows: patrilineal, matrilineal, and bilateral (including states 2, 4, 5, and 6 above) (following ref. 25). *SI Appendix, Fig. S1* shows the descent pattern across extant Bantu cultures. A binary variable was used in the coevolution analyses: patrilineal (ancestral state) versus matrilineal or bilateral, i.e., patrilineal vs. any other state (derived states from Multistate analysis).

For the residence pattern variable 11 of the Ethnographic Atlas (23, 24), transfer of residence at marriage: after first years, was used (following refs. 18 and 19). This variable includes avunculocality within “husband to wife’s group,” but excludes a short stay after marriage by the husband in the wife’s group to perform bride service, capturing the permanent move of one or both marriage partners to a new location (and enables comparison with phylogenetic studies of residence patterns in other language families; refs. 18 and 19). Among Bantu speaking populations, the following three states

are featured 1, wife to husband's group (patrilocal); 2, couple to either group or neolocal; 3, husband to wife's group (matrilocal) (*SI Appendix, Table S1*). *SI Appendix, Fig. S2* shows the residence pattern across extant Bantu cultures. A binary variable was used in the coevolution analyses: patrilocal (ancestral state) versus matrilocal or bi/neolocal i.e., patrilocal vs. all other states (derived states from Multistate analysis).

Phylogeny. We used the most comprehensive Bantu phylogeny available to date based on linguistic data from 542 Bantu languages (9), and consisting of 500 phylogenies from a Bayesian posterior distribution of trees. A maximum clade credibility tree was derived from the full sample, for illustrative purposes, using *TreeAnnotator* (44) and displayed by using *FigTree* (44). A previous analysis (45) using a different Bayesian Bantu phylogeny, based on a different dataset (20), found similar results to those reported here.

Analyses. Phylogenetic signal in data measures the extent to which related taxa are more similar in a particular trait than would be expected by chance. If the signal were low, then it would be difficult to infer the evolutionary history of that trait because the phylogeny gives little or no information on the distribution of the trait among extant populations. The signal in each trait was tested by calculating D using the function *phylo.d* (31) in the *Caper* package (46) in *R* (47). A D value significantly different from random indicates that related populations are more similar in a particular trait than would be expected by chance (31).

A likelihood framework together with Bayesian inference was used to model the evolution of traits along the branches of the tree. Analyses were carried out in *BayesTraits* (available from www.evolution.rdg.ac.uk) (27, 32) using the RJ MCMC procedure. Maximum likelihood analyses of the data, which give point estimates of model parameters, indicated that the prior distributions (the prior belief about the model of evolution) could be best described by an exponential probability distribution because of the small number of changes per unit of branch length. The priors were seeded from exponential hyperpriors (a distribution from which the prior is drawn) with a mean and variance in the range of 0–10 (32). Convergence was checked visually by evaluating changes in the log-likelihood in *Tracer* (48). Each MCMC chain was run five times for 5 million iterations sampled every 100, with the first 50,000 iterations discarded as the burn-in period, to ensure that convergence had been reached. The posterior probabilities for the transition models, rate parameters, log likelihoods, and states at ancestral nodes from the run with the median likelihood taken from the post-convergence portion of each run are reported.

To find the posterior probability distributions of states at ancestral nodes across the phylogenies, an RJ MCMC analysis was run with the additional use of the *addNode* command in *BayesTraits*, which reports the posterior probability of trait states at each internal node on the phylogenetic tree (32). The ancestral state reported for each node of the tree is the combined posterior probability of each state at that node with the posterior probability that the node itself exists in the tree and is plotted on the consensus tree.

The RJ MCMC method used simultaneously travels through the full posterior sample of trees and the universe of all possible models of evolution visiting those models in proportion to their posterior probability. This method provides a posterior probability sample of models of evolution and the rate parameters of the models themselves (27, 49) by visiting the models in proportion to their likelihood and assesses which transition rates, between states, are set to zero (Z) and which are equal to other rate parameters (0, 1, 2).

Discrete, a procedure in *BayesTraits* (27, 32), was used to test hypotheses about correlated evolution between two binary traits. Two models are fitted in this procedure: an independent model in which the two traits evolve over the phylogeny, independent of the state of the other trait, and a dependent model in which the state of one trait affects the probability of change in the other trait. A Bayes Factor (BF) (50) comparison is made between the independent and the dependent models such that independent evolution can be rejected if there is support for the dependent model; support for the dependent model indicates correlated evolution between the traits. For comparisons between models, the \log_{10} BF was calculated, in *Tracer* (48), as twice the difference in the marginal likelihood (32). The BF shows the weight of evidence to support one model over another, from 0–0.5 (insubstantial), to 0.5–1.0 (substantial), to 1.0–2.0 (strong), to >2.0 (decisive) (50). Comparing the transition rates between states indicates the relative timing of the evolution of traits. This method allows for an evaluation of directionality such that the order of evolution can be inferred; by showing which trait evolved first it is possible to test hypotheses explicitly.

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- Parkin R (1997) *Kinship: An Introduction to Basic Concepts* (Blackwell, Oxford).
- Murdock GP (1949) *Social Structure* (MacMillan, New York).
- Hill KR, et al. (2011) Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science* 331(6022):1286–1289.
- Marlowe FW (2004) Marital residence among foragers. *Curr Anthropol* 45(2):277–284.
- Ember CR (1975) Residential variation among hunter-gatherers. *Cross-Cultural Res* 10(3):199–227.
- Diamond J, Bellwood P (2003) Farmers and their languages: The first expansions. *Science* 300(5619):597–603.
- Marck J, Bostoen K (2011) Proto-Oceanic society (Austronesian) and proto-East Bantu society (Niger-Congo) residence, descent, and kin terms, ca. 1000 BC. *Kinship, Language, and Prehistory: Per Hage and the Renaissance in Kinship Studies*, eds Jones D, Bojka M (Univ Utah Press, Salt Lake City), pp 83–94.
- Greenberg JH (1963) *The Languages of Africa* (Indiana Univ Press, Bloomington).
- Currie TE, Meade A, Guillon M, Mace R (2013) Cultural phylogeography of the Bantu Languages of sub-Saharan Africa. *Proc Roy Soc B Biol Sci* 280:1762.
- Russell T, Silva F, Steele J (2014) Modelling the spread of farming in the Bantu-speaking regions of Africa: An archaeology-based phylogeography. *PLoS ONE* 9(1):e87854.
- Maley J, Brenac P (1998) Vegetation dynamics, palaeoenvironments and climatic changes in the forests of western Cameroon during the last 28,000 years B.P. *Rev Palaeobot Palynol* 99(2):157–187.
- Vansina J (1990) *Paths in the Rainforest* (Univ Wisconsin Press, Madison).
- Vansina J (1995) New linguistic evidence and the Bantu expansion. *J Afr Hist* 36(2): 173–195.
- Hage P, Marck J (2011) Proto-Bantu descent groups. *Kinship, Language, and Prehistory: Per Hage and the Renaissance in Kinship Studies*, eds Jones D, Bojka M (Univ Utah Press, Salt Lake City), pp 75–78.
- Divale W (1974) Migration, external warfare and matrilocality. *Behav Sci Res* 9: 75–133.
- Divale W (1984) *Matrilocal Residence in Pre-Literate Societies* (UMI Research, Ann Arbor, MI).
- Heggarty P (2006) Interdisciplinary indiscipline? Can phylogenetic methods meaningfully be applied to language data—and to dating language. *Phylogenetic Methods and the Prehistory of Languages*, eds Forster P, Renfrew C (McDonald Institute for Archaeological Research, Cambridge, United Kingdom), pp 183–194.
- Fortunato L, Jordan F (2010) Your place or mine? A phylogenetic comparative analysis of marital residence in Indo-European and Austronesian societies. *Philos Trans R Soc Lond B Biol Sci* 365(1559):3913–3922.
- Jordan FM, Gray RD, Greenhill SJ, Mace R (2009) Matrilocality is ancestral in Austronesian societies. *Proc Roy Soc B Biol Sci* 276(1664):1957–1964.
- Holden CJ (2002) Bantu language trees reflect the spread of farming across sub-Saharan Africa: A maximum-parsimony analysis. *Proc Biol Sci* 269(1493):793–799.
- Holden CJ, Meade A, Pagel M (2005) Comparison of maximum parsimony and Bayesian Bantu language trees. *The Evolution of Cultural Diversity: A Phylogenetic Approach*, eds Mace R, Holden C, Shennan S (Left Coast, Walnut Creek, CA), pp 53–65.
- de Filippo C, Bostoen K, Stoneking M, Pakendorf B (2012) Bringing together linguistic and genetic evidence to test the Bantu expansion. *Proc Roy Soc B Biol Sci* 279(1741): 3256–3263.
- Gray JP (1999) A corrected ethnographic atlas. *World Cultures* 10(1):24–136.
- Murdock GP (1967) Ethnographic atlas - a summary. *Ethnology* 6(2):109–236.
- Holden CJ, Mace R (2003) Spread of cattle led to the loss of matrilineal descent in Africa: A coevolutionary analysis. *Proc Biol Sci* 270(1532):2425–2433.
- Holden C, Mace R (2005) 'The cow is the enemy of matriliney': Using phylogenetic methods to investigate cultural evolution in Africa. *The Evolution of Cultural Diversity: A Phylogenetic Approach*, eds Mace R, Holden C, Shennan S (Left Coast, Walnut Creek, CA), pp 217–234.
- Pagel M, Meade A (2006) Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo. *Am Nat* 167(6):808–825.
- Mace R, Pagel M (1994) The comparative method in anthropology. *Curr Anthropol* 35(5):549–564.
- Pagel M (1999) Inferring the historical patterns of biological evolution. *Nature* 401(6756):877–884.
- Bastin Y, Coupey A, Mann M (1999) *Continuity and Divergence in the Bantu Languages: Perspectives from a Lexicostatistical Study* (Musée royal de l'Afrique centrale, Tervuren, Belgium).
- Fritz SA, Purvis A (2010) Selectivity in mammalian extinction risk and threat types: A new measure of phylogenetic signal strength in binary traits. *Conserv Biol* 24(4): 1042–1051.
- Pagel M, Meade A, Barker D (2004) Bayesian estimation of ancestral character states on phylogenies. *Syst Biol* 53(5):673–684.

33. Ehret C (2002) *The Civilizations of Africa: A History to 1800* (Univ Press of Virginia, Charlottesville).
34. Gifford-Gonzalez D, Hanotte O (2011) Domesticating animals in Africa: Implications of genetic and archaeological findings. *J World Prehist* 24(1):1–23.
35. Guthrie M (1967–1971) *Comparative Bantu: An Introduction to the Comparative Linguistics and Prehistory of the Bantu Languages* (Gregg Intl, Farnborough, UK).
36. Ember M (1967) The emergence of neolocal residence. *Trans NY Acad Sci* 30(2 Series II): 291–302.
37. Seielstad MT, Minch E, Cavalli-Sforza LL (1998) Genetic evidence for a higher female migration rate in humans. *Nat Genet* 20(3):278–280.
38. Hammer MF, et al. (2001) Hierarchical patterns of global human Y-chromosome diversity. *Mol Biol Evol* 18(7):1189–1203.
39. Destro-Bisol G, et al. (2004) Variation of female and male lineages in sub-Saharan populations: The importance of sociocultural factors. *Mol Biol Evol* 21(9):1673–1682.
40. Ember M, Ember CR (1971) Conditions favoring matrilocal versus patrilocal residence. *Am Anthropol* 73(3):571–594.
41. Howell TL, Kintigh KW (1996) Archaeological identification of kin groups using mortuary and biological data: An example from the American Southwest. *Am Antiq* 61(3):537–554.
42. Dudar JC, Wayne JS, Saunders SR (2003) Determination of a kinship system using ancient DNA, mortuary practice, and historic records in an upper Canadian pioneer cemetery. *Int J Osteoarchaeol* 13(4):232–246.
43. Wu J-J, et al. (2013) Communal breeding promotes a matrilineal social system where husband and wife live apart. *Proc Roy Soc B Biol Sci* 280:1758.
44. Drummond AJ, Rambaut A (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evol Biol* 7(1):214.
45. Opie CF (2013) *The evolution of social systems in human and non-human primates*. DPhil dissertation (University of Oxford, Oxford).
46. Orme C, et al. (2011) caper: Comparative Analyses of Phylogenetics and Evolution in R. Available at cran.r-project.org/web/packages/caper/index.html.
47. R Development Core Team (2008) *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna).
48. Rambaut A, Suchard M, Xie D, Drummond A (2013) Tracer v1.5 Available at beast.bio.ed.ac.uk/Tracer.
49. Currie TE, Greenhill SJ, Gray RD, Hasegawa T, Mace R (2010) Rise and fall of political complexity in island South-East Asia and the Pacific. *Nature* 467(7317):801–804.
50. Kass RE, Raftery AE (1995) Bayes factors. *J Am Stat Assoc* 90(430):773–795.