The Evolution and Ecology of Land Ownership

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Abstract

Land ownership norms play a central role in social-ecological systems, and have been studied extensively as a component of ethnographies. Yet only recently has the distribution of land ownership norms across cultures been examined from evolutionary and ecological perspectives. Here we incorporate evolutionary and macroecological modelling to test associations between land ownership norms and environmental, subsistence, and cultural contact predictors for societies in the Bantu language family. We find that Bantu land ownership norms likely evolved on a unilinear trajectory, but not necessarily one requiring consistent increase in exclusivity as suggested by prior theory. Our macroecological analyses suggest that Bantu societies are more likely to have some form of ownership when their neighbors also do. We also find an effect of environmental productivity, supporting resource defensibility theory, which posits that land ownership is more likely where productivity is predictable. We find less support for a proposed link between agricultural intensification and land ownership. Overall, we demonstrate the value of combining analytical approaches from evolution and ecology to test diverse hypotheses on land ownership across a range of disciplines.

1. Introduction

Cultural norms that govern human relationships with land help shape social-ecological systems. Land tenure systems, particularly land ownership, influence natural resource management, resource distribution, and many traits that comprise cultural diversity. Land tenure has been studied extensively from cultural, political, economic, and natural resource management perspectives (e.g. 1–6), and theories on property rights date back centuries(7–9). The evolutionary and biogeographic dynamics that shape these systems over time and space, however, remain largely a matter of theory. Although land tenure includes several related rights and norms (e.g., usufruct and inheritance), land ownership is a central component and serves as the centerpiece of our analyses. Here we couple biogeographic and evolutionary analyses to investigate temporal and spatial patterns in land ownership norms in a sample of Bantu societies.

How do land ownership norms change over time? Are there fixed trajectories of change, or can any form of land ownership evolve into any other form? Early theories argued for rectilinear trajectories, in which societies progressed in one direction through a series of established stages of land tenure linked to subsistence approaches (e.g. 10,11). The rectilinear model began with a nomadic phase characterized by no land ownership, and continued through a pastoralist phase, in which groups owned land, followed by two agriculturalist phases. In the first, patrilineal kin groups held land; and in the second, individual farmers owned land. Many critiques have emerged regarding strict rectilinear models, including the possibility that societies may progress or regress along the spectrum of different forms of land ownership (no ownership (N), group ownership (G), kin ownership (K), and individual ownership (I)) depending on the cost and benefits of owning land in different forms (12–15). Although less explored, other trajectories may also be possible in which land ownership change is not restricted to shifts up and down the N-G-K-I continuum, but rather any form of ownership can change into any other form if conditions are suitable (see Fig 2a; (16)). Here we use phylogenetic methods adopted from evolutionary biology to distinguish between alternative evolutionary trajectories of land ownership.

Land ownership norms not only vary over time, but also across space (see Figure 1). Long-standing debates spanning multiple academic disciplines still exist regarding which factors shape spatial patterns in land ownership. Here we test three prominent hypotheses. First, cultural norms can be shaped by both vertical (i.e. from one generation to the next) and horizontal (i.e. among individuals within the same generation) cultural transmission. If vertical transmission is prominent, we would expect closely related societies to share similar land ownership norms. If horizontal transmission plays a major role, we would expect societies that are in closer contact (e.g., neighboring groups) to have similar ownership norms. Second, research on territoriality by ecologists, anthropologists, and economists have converged on the theory of resource defensibility (17–23). This theory argues that as the density and predictability of resources increases so to do the benefits of defending these resources, which leads to a greater probability of individuals or groups owning land (6,15,24–26). Third, the use and defense of resources may be linked to subsistence strategies, and certain strategies may work better with specific land ownership norms. For example, communal land ownership may support the transhumance of pastoralist groups that is often associated with high environmental variability (6,27–29). Others suggest that private property co-evolved with agriculture (30), and that increasing intensification of agriculture is also associated with land ownership (6,12). We use a multi-model inference approach to explore the relative power of each of these three sets of factors to predict whether a society possess some form of land ownership (G, K or I) versus none (N).

We focus our analysis on the temporal and spatial variation in land ownership on Bantu-speaking societies, which offers several advantages. A wide range of land tenure systems have historically been employed by Bantu-speaking populations, ranging from individual private ownership to systems in which land is not owned by common individuals or families (e.g. 31–34). The historical relationships among Bantu societies are well-characterized by a language phylogeny(35), making it possible to implement phylogenetic analysis of trait evolution (36). Furthermore, Bantu-speaking societies employ a range of subsistence strategies, from an absence of agriculture to highly intensified agricultural production, making it possible to test the theoretical association between crop cultivation and land ownership.

2. Materials and methods

2.1 Data

The data for this study include land ownership norms coded for 73 societies that are included in the reference phylogeny for Bantu (35), and for which Ethnographic Atlas data and environmental variables are available through the D-PLACE database (37–43) (See supplementary material for full dataset). This constitutes a maximal sample of Bantu-speaking societies for which both phylogenetic and cultural information are available. Variables describing the annual mean and variance for temperature and precipitation in D-PLACE are from the Baseline Historical (1900–1949) CCSM ecoClimate model (spatial resolution of 0.5°; (40)). Monthly net primary productivity (NPP) reflect annual mean, variance and constancy from data obtained from the MODIS dataset (spatial resolution of 1 km; (41)). Elevation and distance to coast in D-PLACE are from the Global Multi-resolution Terrain Elevation Data of the U.S. Geological Survey (44). Agricultural intensity represents the Ethnographic Atlas variable EA028 (37,38). We recoded EA028 as a binary variable expressing the presence or absence of intensive agriculture.

We coded land tenure data based on ethnographic descriptions of each society (see supplementary materials). Following the coding procedures of Kushnick et al. (16), we coded each society's primary land ownership norm as no ownership (N), group ownership (G), kin ownership (K), or individual ownership (I). The land ownership variable used in this study thus encodes the land holding available to a majority of people in a particular society according to documented traditional or customary norms. We focus here on the earliest norms recorded in ethnographic literature to avoid, to the extent possible, known impacts of post-colonial political, economic, and social change (45). Where land tenure norms were described as undergoing transition, we coded those norms noted to be customary or to have pre-dated colonial influences. Our coding strategy departs from that described in Kushnick et al. (16) in that we do not consider ownership norms restricted to elite classes to be the main type of ownership in a society unless that norm is also available to ordinary members of the society. The land ownership variable presented here can thus be thought of as a majority land ownership norm.

To avoid problems of multicollinearity in environmental data we used principal component analysis (see supplementary materials, Fig S1). Based on eigenvalues, we used three components to capture the variability in environmental conditions across the region (Table S3). We refer to these components as environmental productivity, mountains, and productivity uncertainty. Following Vilela et al (46), the other composite variable included in this study characterizes each society's reliance on agriculture for subsistence, derived from a principal component analysis on Ethnographic Atlas variables that characterize dietary reliance on specific subsistence activities (see supplementary materials).

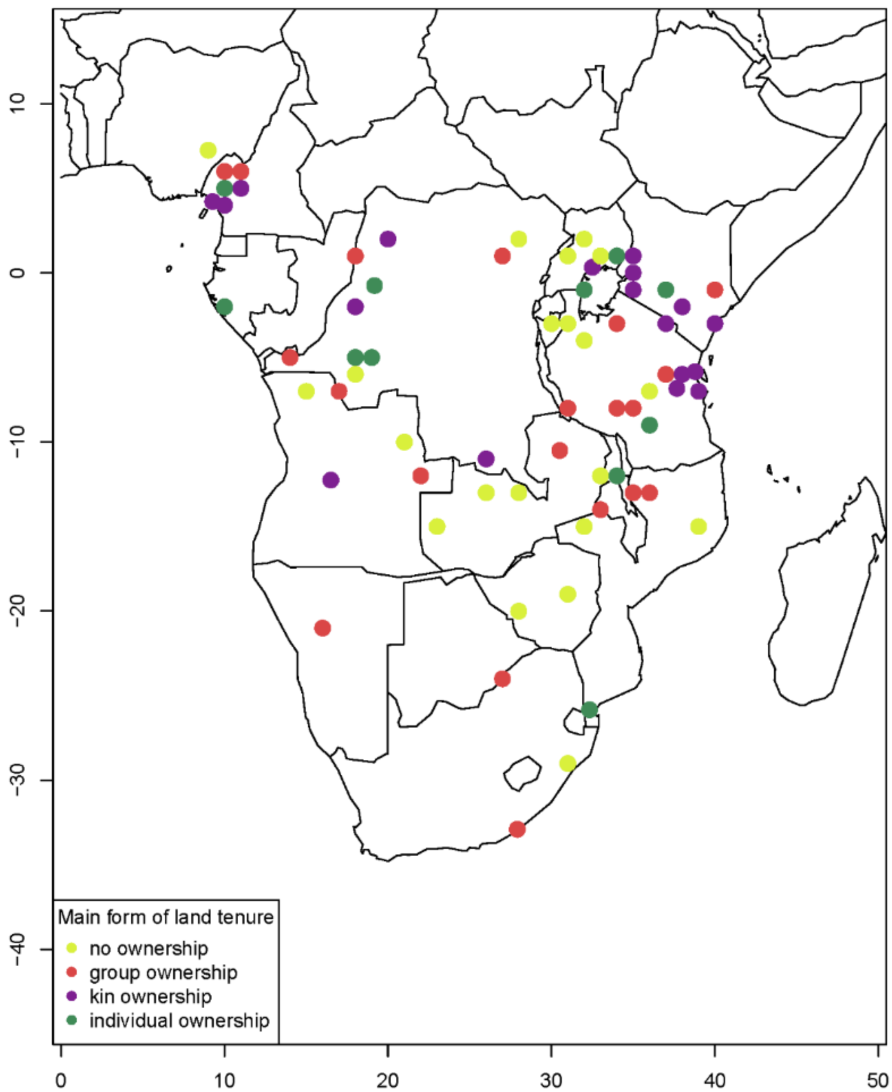

Figure 1: Land tenure norms associated with a majority of the population of societies in the sample (n= 73).

2.2 Phylogenetic analyses of evolution of land ownership

We characterized the evolution of land ownership by measuring phylogenetic and geographic signal in the trait data, and modeling alternative evolutionary trajectories using maximum likelihood methods. These analyses paired land tenure data described above with Bantu language trees produced by Grollemund et al. (35). A 2,000 tree posterior sample from Bayesian Markov Chain Monte Carlo (MCMC) analysis on cognate data across 100 meanings in 424 Bantu and Bantoid languages (35) was pruned to retain only the 73 taxa for which land ownership data were available. We computed a maximum clade credibility (MCC) tree for this pruned tree sample using the *TreeAnnotator* package of BEAST v.2.4.7 (47). We used this MCC tree for the purposes of phylogenetic signal estimation. We performed model comparisons to test support for alternative evolutionary trajectories using the full 2,000 tree sample.

We characterized the phylogenetic signal in land ownership using the D statistic for binary characters (48). This statistic uses the sum of sister-clade differences to characterize the distribution of observed trait states across taxa and measures the similarity of the observed trait distribution to the expected for different processes. D = 0 resembles a distribution as expected under a Brownian Motion, whereas D = 1 resembles expectations under random conditions, which may be due to fast evolutionary processes, for example. Negative values of D indicate more clumping than expected by Brownian motion model, and values above 1 indicate more dispersed trait values than expected just by chance. We estimated the D statistic and associated p-value for each land tenure norm on the MCC tree and the full tree sample using the *caper* package for R (49). Following Kushnick et al. (16) we also calculated the D statistic on a tree derived by hierarchical clustering on geographic distances to estimate the degree of geographic organization in each individual ownership norm's distribution.

We used the *MultiState* phylogenetic comparative method of the *BayesTraits V3* software package to evaluate possible evolutionary trajectories for land ownership norms (50,51). This method uses a continuous-time Markov model to infer the evolution of a categorical trait on the trees in a given tree sample. In this method transition rate parameters express the probabilities of changes from each state to any other state for the trait of interest. We use these parameters to model alternative trajectories for the evolution of ownership, setting certain parameters to zero values to reflect the impossibility of a particular transition under a given theoretical model. We used maximum likelihood analyses without a covarion to estimate model parameters. Likelihood scores for each model and each tree in the sample were used to calculate Akaike Information Criterion values (AIC = 2k-2lnLh, where k is the number of unrestricted parameters).

We evaluated the same set of candidate models of land ownership trait evolution as Kushnick et al. (16). Each model expresses a possible trajectory for changing land ownership norms (Fig. 2a). This set of trajectories includes a full model, in which all 12 possible transitions from one state to another are allowed, as well as multiple variations on progressive and non-progressive models. For progressive models, both an Exclusivity Gain trajectory (N-G-K-I) and an Alternative trajectory (N-I-G-K) were explored. Progressive models are characterized as Rectilinear (sequential changes in a single direction), Unilinear (sequential changes in either direction), or Relaxed Unilinear (sequential changes in either direction, plus transitions from any state to N). Among the non-progressive models, the No Loss model allows all transitions except changes to non-ownership from any other state. The Loss for Change model allows transitions in either direction between Non-Ownership and each other state, but no transitions between G, K, and I. The Gain from None model is further restricted to allow only transitions from non-ownership to any other state, while disallowing changes in the other direction. The Unstable Group model allows transitions to group only from non-ownership but allows all possible transitions between other pairs of states. The Kin-Group model allows all possible transitions except for any transition away from kin. Finally, the Corporate model requires that once kin or individual ownership arises, only transitions between these two states are allowed. All other transitions are possible under this model.

2.3 Multi-model inference of drivers of spatial patterns in land ownership

The expansion of Bantu across the central and southern regions of Africa brought speakers of these languages into a range of environments from forests to savannas and put them in contact with other cultures, including hunter-gatherer and pastoralist populations. To test the relative influence of possible environmental, subsistence, and contact-related predictors on Bantu land ownership norms, we applied a multi-model inference approach based on logistic regression to model the presence of land ownership in

Bantu societies (15,52). For this analysis we recoded land ownership as a binary variable (0 = no ownership; 1 = group, kin, or individual ownership).

The full model in this analysis predicted land ownership as a function of intensive agriculture, reliance on agriculture, environmental productivity, productivity uncertainty, mountains, distance to coast, and a neighbor effect. The neighbor effect expresses the proportion of the eight closest spatial neighbor societies that shares a given society's primary land ownership norm, and it serves as a proxy for horizontal transmission of land ownership norms. We centered (by subtracting mean) and scaled (by standard deviation) all continuous variables included in the model using the scale function in R(53). We also included language classification information from Glottolog (Narrow Bantu subgroups Ababuan, Bantu-A-B10-B20-B30, Central Western Bantu, and East Bantu as well as the Southern Bantoid classifications Tivoid and Wide Grassfields) as a random effect to account for shared ancestry (54–56). Due to missing data for at least some of the variables of interest, we excluded 8 societies from the analysis of spatial variation, resulting in a sample size of 65 societies (see supplementary materials).

We used multimodel inference (52) to examine all possible alternative models involving subsets of the fixed and random effects in this full model (Table S6). This was carried out using the *MuMIn* package for R (57). We implemented model averaging based on AIC weights to account for uncertainty across multiple competing models.

Two societies in the sample were non-agriculturalists. The Mbuti are generally considered a hunter-gatherer group, and the Herero rely largely on pastoralism. In addition, three other societies (Lozi (which use substantial animal husbandry and hunting), Sangu (for which animal husbandry is the other primary activity), and the Ngala (which have a high reliance on fishing) rely on agriculture for less than 50% of their subsistence (based on the Ethnographic Atlas variable EA005; (37,38)). Two of our independent variables focus on reliance on agriculture and intensive agriculture, both of which may be as relevant for these societies. In turn, we also ran our multimodel inference analysis with a sample that excluded these 5 societies (n = 60).

3. Results

3.1 Evolutionary trajectories of land ownership

D statistic values for non-ownership (D = 0.73) and group ownership (D = 0.75) are significantly different from 0 (p <.05) on the MCC tree, as well as on the full tree (see supplementary materials), suggesting a lack of phylogenetic signal for these forms of land tenure. The D-statistic for individual land ownership (D = 1.13) is also significantly different from 0 (p = 0.009) on the MCC tree and full posterior sample (see supplementary materials), but a D statistic greater than 1 indicates overdispersion of this trait. Kin ownership has a relatively low, positive D statistic (D = 0.20) that is significantly different from 1 (p = 0.005), indicating moderate phylogenetic signal for this trait. All land tenure types have positive D statistics that are significantly different from 0 on the geographic tree, suggesting that no significant geographic "clumping" exists for any specific land ownership norm (see supplementary materials).

Based on AIC evidence, the Alternative Unilinear model best fits the patterns we see in land ownership in Bantu-speaking societies (Fig. 2b). Like the best models reported for the evolution of land tenure in Austronesian societies (16), this model implements a N-I-G-K trajectory that departs from the constant increase in exclusivity proposed in prior literature to explain the evolution of land tenure. However, we also find some support for the Exclusivity Gain configuration of the Unilinear model (ΔAIC = 0.497), which does restrict the trajectory of change in this trait to the traditional N-G-K-I pathway. The Loss for Change model, which does not allow transitions between G, K, and I, finds a similar level of support (ΔAIC = 0.497). All other models are not supported by our results (ΔAIC >2).

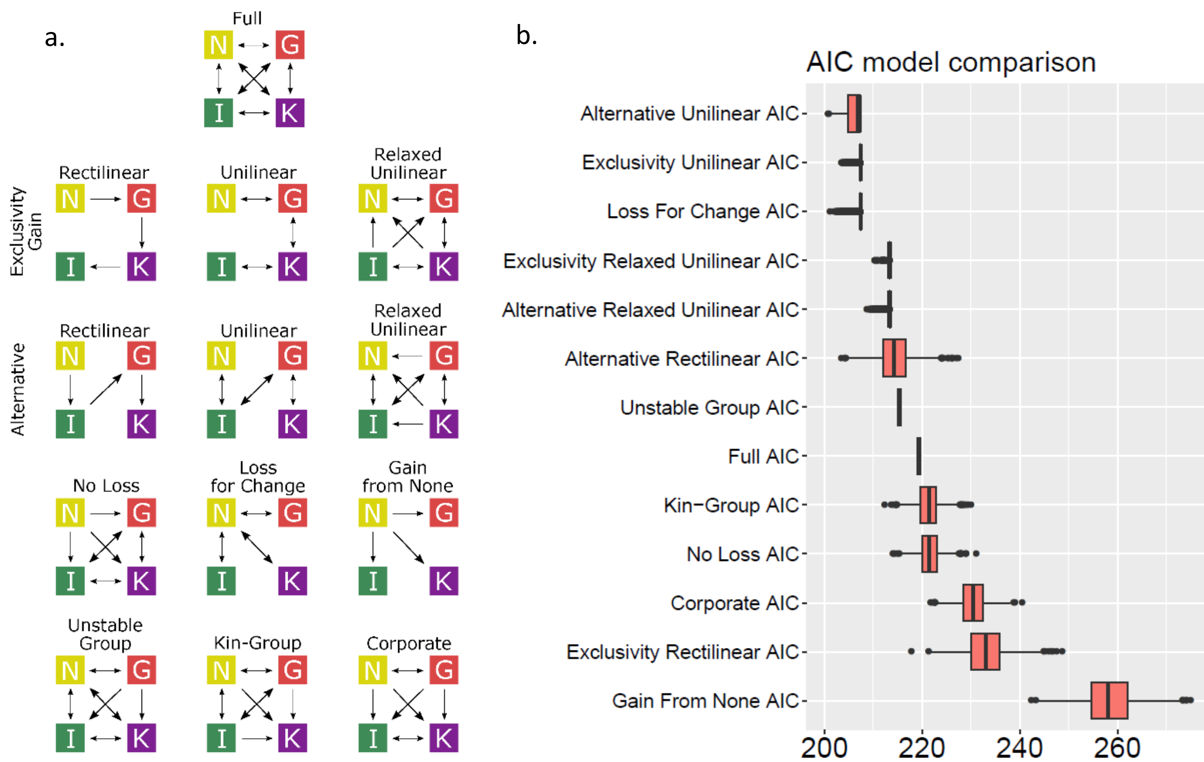

Figure 2: a) Models of land ownership change considered in phylogenetic analysis; b) AIC values for alternative models on 2,000 tree posterior sample.

3.2 Drivers of spatial variation in land ownership

To evaluate influences other than evolutionary tendencies on the land ownership norms of these societies, we used a multimodel averaging approach based on logistic regression, as described in Section 2.4. The AICw of the best model is 0.09 (see Table S5 in supplementary materials), suggesting that model averaging is an appropriate method for this study (52). Neighbor effect (proportion of neighboring societies with private ownership) is an important predictor of land ownership in this sample, occurring in all models with ΔAIC < 2. The relatively large multimodel average effect size for this variable (Table 1) suggests that the land ownership practices of neighboring societies are important for predicting land ownership norms.

We also find evidence that land ownership might be more likely to occur where resource productivity is predictable; productivity uncertainty occurs in several models with ΔAIC < 2 and is associated with a relatively small, negative coefficient in the averaged model. All other environmental variables contribute to a lesser extent to the averaged model, suggesting that they may play only a minor role in land ownership practices.

While we may have expected that agriculture, and in particular intensive agriculture, should be an important predictor of land ownership (12), we find that reliance on agriculture and intensive agriculture are associated with relatively small effect sizes and relatively low importance in the averaged model. While it is theoretically possible that redundancy in the characterization of subsistence may interfere with the identification of meaningful effects, no multicollinearity issues are identified in this dataset (VIF < 2 for all variables; reliance on agriculture VIF = 1.53, intensive agriculture VIF = 1.36). This suggests that the relationship between the cultivation of crops and the protection of territory through land ownership is indeed less important than we would have expected. When we omitted the five societies that did not rely on agriculture for the majority of their subsistence (n = 60 societies, see Methods), results were qualitatively similar to those presented here for the full sample (n = 65) (see Tables S7 and S8).

We used R^2_{GLMM} to measure marginal and conditional fit of the averaged model reported in the main text. Marginal R^2_{GLMM} is 0.59 and conditional R^2_{GLMM} is 0.61, suggesting that the language subgroup random effect does not account for a large proportion of the variation in land ownership. We found no evidence of spatial autocorrelation in model residuals (Moran's I = -0.006, p = 0.3).

Table 1: Multi-model average for models of land ownership (full average). *Intensive agriculture coded as binary (presence/absence of intensive agriculture; absence of intensive agriculture treated as reference level). Land ownership coded as binary (presence/absence of any land ownership available to a majority of the society's population; absence of ownership for most community members treated as reference level). Standardized coefficients are presented. Marginal R^2_{GLMM} = 0.59, conditional R^2_{GLMM} = 0.61*

Parameter	β coefficient	Standard error	z value	RVI
(Intercept)	-3.019	1.268	2.337	1.00
Neighbor Effect	7.404	2.165	3.353	1.00
Productivity Uncertainty	-0.271	0.385	0.697	0.50
Reliance on Agriculture	0.415	0.824	0.497	0.37
Intensive Agriculture	-0.353	0.754	0.463	0.35
Distance to Coast	-0.111	0.314	0.350	0.32
Mountains	-0.067	0.249	0.266	0.28
Productivity	0.019	0.144	0.132	0.26

4. Discussion

Our results provide new insights on the various pressures that impact land tenure over time and space. We find that unilinear trajectories and reversion to non-ownership in the process of change are potentially more consistent with Bantu land tenure patterns than alternative trajectories. We find evidence for a trajectory in which individual ownership may follow non-ownership on such a trajectory, contrary to expectations that ownership should evolve along a trajectory of increasing exclusivity of rights (cf. 10,11,13,16). Our results are similar to those for Austronesian societies reported in the only other phylogenetic-based analysis of land ownership to date (16). That we find evidence for this alternative pathway in a second major ethnolinguistic family suggests that the development of individual ownership norms directly from systems without any ownership may not be a tendency of a single set of related cultures but rather a more general pattern in the way land tenure systems develop over time.

We find support for multiple possible evolutionary pathways. This lack of resolution in the pathway analyses may, in part, be due to localized horizontal transfer. Our macroecological analyses find an influence of neighbors on land tenure strategies, and these localized horizontal transmission events may make it difficult to distinguish specific evolutionary pathways across the whole tree.

One longstanding idea about other influences on land tenure focuses on the relationship between this trait and subsistence practices (12,58–60). These theories propose that agricultural development and land ownership co-evolve, and might predict that societies with intensive agriculture would be particularly likely to recognize some form of land ownership. However, reliance on agriculture and intensive agriculture are not particularly important predictors of land ownership in our averaged model.

This result might be especially surprising from the perspective of traditional unilinear cultural evolution theories that tie agriculture and land tenure together on a progressive pathway toward cultural complexity. Among the 65 societies included in the relevant analysis, we find five that practice intensive agriculture but do not have land ownership. In most of these, including Lozi, Nyoro, and Soga, land is controlled by a king or chief and usufruct rights, but not ownership, are granted to individuals and families (32,34,61). Although private citizens are allowed to live on and cultivate parcels of land, typical ownership rights such as the sale or rental of land are prohibited in these societies and in many cases land can be withdrawn from users and reassigned. It has been suggested that scarcity of arable land is a factor in the customary Bantu land tenure systems that allow ownership by common individuals or groups versus those that do not (31). This is consistent with more recent ideas about the evolutionary ecology of territoriality and real property, namely that scarcity of land is crucial to balancing resource-related benefits against the social and economic costs of long-term, exclusive control of land (62). With only two non-agricultural groups included in this sample (Mbuti and Herero), we are unable to draw comparisons about how land tenure norms in foraging or pastoralist societies compare to agriculturalist land ownership. However, our results suggest that agricultural cultivation does not predict the privatization of land ownership, but rather plays a modest role within a more complex suite of influences.

Early tests of resource defensibility theory, based largely on qualitative case studies or limited sample sizes, produced mixed results (17,21,63). More recently, Ember et al.(6) and Kavanagh et al.(15) found some support for resource defensibility theory in societies spread across the globe and using a range of different subsistence strategies. However, Freeman and Anderies (64) concluded that less predictable and less dense resources increased the probability of land ownership in hunter-gatherer societies. Here we find that uncertainty of productivity is negatively associated with land ownership. In other words, land ownership is more likely in locations where productivity is predictable. This echoes prior research which suggests that predictability of resources is a factor in determining whether resource defense is economically viable (6,15,65). Private ownership of land may facilitate the defense of natural resources in environments where those resources are reliable enough to justify such actions.

The most important predictor of land ownership in our averaged model is the neighbor effect, which measures the proportion of neighboring societies that share similar ownership norms with a given society. Although none of the four norms of ownership (N, I, G, K) is individually clustered in space, as demonstrated by the measurement of geographic signal for each norm using the D statistic, our results indicate that societies may be more likely to have some form of ownership when nearby societies have any form of ownership. Indeed, the neighbor scores for societies that do have a majority norm of land ownership are significantly higher, on average, than the neighbor scores for societies without land ownership (mean = 0.73 for societies with ownership; mean = 0.40 for societies without ownership; $t = -6.025$, $df = 37.205$, $p < 0.001$). Societies may adopt land ownership norms from nearby groups via direct observation or through horizontal cultural transmission mechanisms. However, we also cannot rule out the possibility that other mechanisms lead to similar norms among neighboring groups, including possible effects of other spatially-clustered environmental or social conditions (such as increased competition between groups within a given geographical location) that our data do not currently capture.

Overall, we have used a combination of evolutionary and macroecological analyses to conclude that land ownership in Bantu-speaking societies is shaped by a complex set of forces that operate in cultural, environmental, and historical context.

Data Accessibility

All data are available from www.d-place.org and are listed in tables in the supplementary materials.

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Supplementary Materials

Land tenure coding

Land tenure was coded for a sample of societies that represents the maximal overlap between the Grollemund et al. (2014) Bantu language phylogeny, the Bantu societies included in the Ethnographic Atlas, and the societies for which published ethnographies were accessible. This sample reflects a compromise between completeness of data, sample size, and coding effort.

Land tenure has been coded in many ways in prior research (e.g. 10,13,14,16). We adopt the system described in Kushnick et al.(16) for two reasons: 1) this system focuses on land *ownership* norms, and 2) this system of representing each society with the norm that applies to a majority of its population is compatible with the analytical techniques we used. We adapted this system for our uses by not including forms of land ownership restricted to elites (kings, political leaders) as primary forms of land tenure.

The variable created through this coding process encodes the primary land ownership norm for each society as a categorical variable. We define the primary land ownership norm as the norm associated with the majority of people in a society at the time of ethnographic description. Where multiple norms apply to an entire population we considered the extent and use of lands associated with each norm to determine which was the primary norm. For example, a society with kin ownership of farming lands but collective (group) ownership of ceremonial sites would be coded as K (kin).

This schema categorized societies into four categories of land ownership. Non-ownership describes societies in which the majority of people own no land. Usufruct rights may be granted to individuals, kin groups, or other groups in non-ownership societies, but crucially land is not owned or is held in trust for the community by a ruler or leader. Group ownership describes societies in which land is owned by groups of related and unrelated individuals, such as villages. In kin ownership societies a majority of people own land as part of kin groups, such as lineages or bilateral kin groups. Individual ownership indicates that the majority of individuals in a society are able to hold land. We collected additional information on elite ownership (land holding by rulers or members of privileged classes) and on the existence of multiple norms in a society. However, our coding of data for these analyses assigned exactly one primary norm (N, G, K, or I) to each society in the sample.

All land tenure coding was completed by two coders. Duplicate coding of 17 societies in the sample was used to confirm an acceptable level of inter-coder reliability; the remainder of the dataset was coded by a single coder. Inter-coder reliability for the independent categorization of the main land ownership norm in the 17 societies coded by both coders was 76%. Cases involving coder disagreement were revisited by the team to reconcile differences, resulting in full resolution of all coding differences in this sample through discussion (100% agreement). Subsequent to this inter-coder reliability test and training, all difficult coding decisions were discussed by at least two members of the research team to ensure a high level of consistency in the data.

See Kushnick et al. (2014) for further discussion of the practicalities of land tenure coding and the representation of primary land ownership norm as a single multistate trait in phylogenetic comparative methods.

522 *Table S1: Primary land ownership norms and identifying information for Bantu societies in sample.*
523 *n=73.*

D-PLACE Society Name	Bantu Language Taxon Name	EA ID	Primary Land Ownership	Source	Date Range
Mbuti	D211_Kango	Aa5	N	Putnam 1963	ca. 1940-1960
Lozi	K21_Lozi	Ab03	N	Prins 1980	1876-1896
Tsonga	S53_Tsonga	Ab04	I	Junod 1927	1895-1927
Herero	R31_Herero	Ab1	G	Vedder, H. 1928	Pre-1925
Xhosa	S41_Xhosa	Ab11	G	Soga 1932	ca. 1930-1939
Zulu	S42_Zulu	Ab12	N	Cetewayo et al. 1978	1800-1884
Tswana	S31_Tswana	Ab13	G	Schapera 1953	ca. 1950
Shona	S11_Shona	Ab18	N	Bullock 1950	1901-1949
Mbundu	R11_Umbundu	Ab5	K	McCulloch 1952	ca. 1950
Ndebele	S44_Ndebele	Ab9	N	Kuper 1955	1872
Chewa	N31_Chewa	Ac10	G	Hodgson 1933	ca. 1933
Luvale	K14_Lwena	Ac11	G	White 1955	ca. 1950
Chokwe	K11_Ciokwe	Ac12	N	McCulloch 1951	Pre-1951
Tonga	M64_Tonga	Ac13	I	Van Velsen 1964	1930-1952
Bakongo	H16a_Kisikongo_2013	Ac14	N	Weeks 1913	1900-1915
Mbala	H41_Mbala	Ac15	I	Torday and Joyce 1905	ca. 1900
Suku	H32_Suku	Ac17	N	Kopytoff 1965	ca. 1950-1960
Sundi	H131_Kisundi_Congo_Kimongo_1988	Ac18	G	Laman 1953	1891-1919
Yaka	H31_Yaka	Ac20	G	Torday 1906	1906
Bunda	B84_Mbunda	Ac21	I	Torday 1905	ca. 1900
Songo	B85d_Nsongo	Ac25	K	Richards 1950	ca. 1950
Bemba	M42_Bemba	Ac3	G	Richards 1939	ca. 1939
Kaonde	L41_Kaonde	Ac32	N	Watson 1954	Pre-1952
Kunda	N42_Kunda	Ac37	N	Bruwer et al 1958	Pre-1955
Nyasa	N11_Manda	Ac39	G	Johnson 1922	Pre-1920
Makua	P31_Emakhua	Ac42	N	Tew 1950	ca. 1950
Lamba	M54_Lamba	Ac5	N	Doke 1931	ca. 1930
Ndembu	L52_Lunda	Ac6	K	Turner 1957	ca. 1957
Yao	P21_Yao	Ac7	G	Mitchell 1952	1946-1949
Ngoni	N12_Ngoni	Ac9	N	Barnes 1954	ca. 1950
Nyoro	JE11_Runyoro	Ad02	N	Beattie 1971	Pre-1950
Kikuyu	E51_Kikuyu	Ad04	I	Kenyatta 1953	1920-1938
Gisu	JE31_Lumasaaba	Ad09	I	La Fontaine 1959	1890-1954
Bena	G63_Bena	Ad11	I	Culwick et al. 1935	1928-1933
Gusii	JE42_Gusii	Ad12	K	Mayer 1949	1946-1948
Luguru	G35_Luguru	Ad14	K	Beidelman 1967	ca. 1960
Fipa	M13_Fipa	Ad19	G	Willis 1966	ca. 1966
Sukuma	F21_Sukuma	Ad22	G	Malcolm 1953	ca. 1950-1959
Sangu	G61_Sangu	Ad23	G	Mumford 1934	Pre-1930
Gogo	G11_Gogo	Ad24	N	Rigby 1966	ca. 1960-1969
Kwere	G32_Kwere	Ad27	K	Beidelman 1967	ca. 1960
Zigula	G31_Zigua	Ad28	K	Biedelman 1967	1894
Chagga	E622A_Kimochi	Ad3	K	Stahl 1964	1960
Giriama	E72a_Giryama	Ad32	K	Barrett 1911	ca. 1911
Pokomo	E71A_Upper_Pokomo	Ad33	G	Prins 1952	ca. 1950
Kamba	E55_Kamba	Ad34	K	Middleton and Kershaw 2017	1920-1947
Meru	E53_Meru	Ad35	K	Middleton 1965	Pre-1929

Vugusu	JE31c_Bukusu	Ad41	K	Wagner 1949	Pre-1940
Haya	JE22_Haya	Ad42	I	Cory and Hartnoll 1971	ca. 1970
Soga	JE16_Lusoga	Ad46	N	Roscoe 1911	ca. 1911
Sumbwa	F23_Sumbwa	Ad47	N	Forde and Abrahams 1967	Pre-1967
Toro	JE12_Rutooro	Ad48	N	Forde 1962	Pre-1950
Zinza	JE23_Zinza	Ad49	N	Forde and Taylor 1962	Pre-1962
Kaguru	G12_Kagulu	Ad50	G	Beidelman 1967	1967
Ngulu	G34_Nguungulu	Ad51	K	Beidelman 1967	ca. 1960
Ganda	JE15_Luganda	Ad7	K	Roscoe 1902	ca. 1900
Hehe	G62_Hehe	Ad8	G	Brown and Hutt 1935	ca. 1935
Nkundo	C61_Mongo	Ae04	I	Hulstaert & Vizedom 1938	1930-1938
Rundi	JD62_Rundi	Ae08	N	Meyer & Handzik 1916	1812-1911
Duala	A24_Duala	Ae12	K	Ardener 1956	ca. 1955
Kpe	A22_Bakweri	Ae2	K	Ardener 1957	ca. 1950
Ekonda	C61E_Konda	Ae20	K	Brown 1944	ca. 1944
Ngala	C36d_Lingala	Ae28	G	Weeks 1913	1890
Ndaka	D21_Baali	Ae33	G	Schebesta 1933	1929-1930
Ngombe	C41_Ngombe	Ae39	K	Wolfe 1961	ca. 1960
Mpongwe	B11a_Mpongwe	Ae46	I	Burton 1968	ca. 1968
Bafia	A53_Bafia_rikpa	Ae48	K	Dugast et al 1954	ca. 1950
Bali Nyonga	Mungaka_Grassfields	Ae49	G	Covarrubias 1937	Pre-1937
Bamileke	Fefe_Grassfields	Ae5	I	Littlewood 1954	ca. 1950
Bamun	Bamun_Grassfields	Ae50	G	Littlewood 1954	ca. 1910-1950
Kom	Kom_Grassfields	Ae54	G	Jefferys 1951	ca. 1950
Widikum	Moghamo_Grassfields	Ae59	K	Kaberry 1952	ca. 1950
Tiv	Tiv_Tivoid	Ah03	N	Bohannan 1968	1907-1953

Societies excluded from multimodel inference due to missing data

The following societies were removed from the sample prior to biogeographic analysis as a result of missing data:

Tonga (Ac13)
Mbala (Ac15)
Nyasa (Ac39)
Makua (Ac42)
Haya (Ad42)
Bali Nyonga (Ae49)
Kom (Ae54)
Widikum (Ae59)

Table S2. Data on cultural and environmental variables for all Bantu included in the evolutionary and multimodel inference analyses

ID	DPLACE Name	Glottolog Subgroup	Main Land Tenure Norm	Reliance on Agric.	Intensive Agric.	Lat.	Long.	Elev.	Slope	Annual Mean Precip.	Annual Precip. Variance	Annual Mean Temp.	Annual Temp. Variance	Monthly Mean NPP	NPP Variance	Distance to coast
Aa5	Mbuti	Ababuan	N	-1.58	0	2	28	805	0.60	243308	9483286472	21.42	0.31	3.49	1.60	1448.49
Ab1	Herero	Central-Western-Bantu	G	-0.24	0	-21	16	1442	0.90	52226	4874838526	21.99	7.87	0.43	0.18	217.22
Ab11	Xhosa	East-Bantu	G	0.55	0	-32.9	27.9	445	1.82	96542	3179657454	17.10	8.93	2.86	1.22	10.78
Ab12	Zulu	East-Bantu	N	0.90	0	-29	31	281	2.43	165894	11178307664	16.45	8.37	2.74	0.82	52.92
Ab13	Tswana	East-Bantu	G	0.85	0	-24	27	976	0.78	78321	5544617497	18.42	14.38	0.89	0.32	596.05
Ab18	Shona	East-Bantu	N	0.29	0	-19	31	1310	0.99	80001	9844635651	18.62	12.61	1.83	0.56	388.32
Ab3	Lozi	East-Bantu	N	0.09	1	-15	23	1048	0.20	116188	18444498077	21.27	9.70	1.18	0.87	1055.19
Ab4	Tsonga	East-Bantu	I	0.63	0	-24	32	168	0.49	102638	10551815964	20.20	9.70	1.37	0.33	189.43
Ab5	Mbundu	Central-Western-Bantu	K	0.29	0	-12	16	1655	1.21	122623	13467979126	17.79	2.70	2.36	0.92	241.11
Ab9	Ndebele	East-Bantu	N	0.87	0	-20	28	1290	0.79	81721	10979414178	19.92	13.82	1.46	0.78	695.71
Ac10	Chewa	East-Bantu	G	-0.06	0	-14	33	1037	1.84	106647	15053921231	19.14	11.42	2.14	1.19	595.32
Ac11	Luvale	Central-Western-Bantu	G	-0.10	0	-12	22	1080	0.07	140787	19771051651	20.23	5.38	0.85	0.43	893.23
Ac12	Chokwe	Central-Western-Bantu	N	0.09	0	-10	21	1090	0.64	130821	13961412818	20.50	2.80	1.79	1.37	789.17
Ac14	Bakongo	Central-Western-Bantu	N	0.15	0	-7	15	1001	1.25	104336	7683087818	22.15	0.97	2.57	0.66	224.08

Ac17	Suku	Central-Western-Bantu	N	-0.20	0	-6	18	875	1.28	138863	9110469846	21.48	0.74	1.63	1.01	572.91
Ac18	Sundi	Central-Western-Bantu	G	0.14	0	-5	14	401	1.55	134134	8573238351	23.37	0.72	2.00	0.75	184.70
Ac20	Yaka	Central-Western-Bantu	G	0.39	0	-7	17	639	1.39	111927	7184397498	21.53	0.94	1.85	1.10	426.57
Ac21	Bunda	Central-Western-Bantu	I	0.42	0	-5	19	643	1.53	158148	10819803484	22.74	0.56	1.30	0.94	709.88
Ac25	Songo	Central-Western-Bantu	K	-0.05	0	-5	18	599	1.90	151544	9502551210	22.34	0.57	1.66	1.20	600.72
Ac3	Bemba	East-Bantu	G	-0.08	0	-11	31	1332	0.75	121032	19280474471	17.73	9.60	2.50	1.16	944.41
Ac32	Kaonde	Central-Western-Bantu	N	-0.25	0	-13	26	1269	0.65	130320	21038146658	18.57	10.60	2.18	1.96	1179.43
Ac37	Kunda	East-Bantu	N	-0.19	0	-15	32	656	1.81	94551	14090898866	22.44	11.09	1.63	1.07	585.57
Ac5	Lamba	East-Bantu	N	-0.17	0	-13	28	1222	0.61	123074	20070415029	17.72	11.93	2.05	1.59	1021.30
Ac6	Ndembu	Central-Western-Bantu	K	0.24	0	-11	26	1497	0.84	146960	23765211571	18.28	7.46	2.15	1.66	1326.30
Ac7	Yao	East-Bantu	G	0.25	0	-13	36	711	1.09	108717	14422661246	19.98	7.86	2.27	1.00	476.87
Ac9	Ngoni	East-Bantu	N	0.27	0	-12	33	1182	0.89	108968	16053942987	19.36	10.26	1.94	0.69	764.28
Ad11	Bena	East-Bantu	I	0.82	1	-9	36	585	1.95	118309	12754658363	18.97	6.44	2.45	0.76	365.88
Ad12	Gusii	East-Bantu	K	1.05	0	-1	35	1772	1.28	71490	6601926733	19.02	1.64	2.59	0.34	605.34
Ad14	Luguru	East-Bantu	K	0.40	0	-8	38	230	0.82	110656	7589578679	23.71	2.94	1.46	0.38	135.21
Ad19	Fipa	East-Bantu	G	0.33	0	-8	31	1466	2.17	123075	18758274140	18.85	5.12	2.19	0.90	884.63
Ad2	Nyoro	East-Bantu	N	0.62	1	2	32	1057	0.40	144039	15069126112	22.58	1.30	1.92	0.70	1050.80

Ad22	Sukuma	East-Bantu	G	1.05	1	-3	34	1342	0.50	100790	14915127800	20.38	1.69	1.38	0.55	605.38
Ad23	Sangu	East-Bantu	G	0.88	1	-8	34	1186	1.04	103942	13978275716	18.35	6.06	1.81	0.72	564.02
Ad24	Gogo	East-Bantu	N	0.89	0	-7	36	1082	4.73	105667	10965837982	19.46	4.98	2.08	0.46	321.80
Ad27	Kwere	East-Bantu	K	0.41	0	-7	39	84	0.46	111773	4935576660	24.30	2.85	2.00	0.21	34.94
Ad28	Zigula	East-Bantu	K	0.58	0	-5.8	38.8	146	0.59	111335	4389031613	22.36	2.85	1.85	0.16	3.51
Ad3	Chagga	East-Bantu	K	0.86	1	-3	37	1403	3.02	69842	3910439083	19.05	2.86	2.23	0.14	306.80
Ad32	Giriama	East-Bantu	K	0.73	0	-3	40	20	0.20	77809	3537188378	25.39	1.74	1.56	0.23	18.48
Ad33	Pokomo	East-Bantu	G	-0.03	1	-1	40	88	0.09	58571	2579307447	26.09	2.78	0.69	0.11	134.52
Ad34	Kamba	East-Bantu	K	0.97	1	-2	38	680	0.99	70370	2466144649	19.36	2.88	1.32	0.23	256.42
Ad35	Meru	East-Bantu	K	0.79	0	0	35	1848	2.15	68198	6129817057	19.40	1.24	4.39	0.24	651.60
Ad4	Kikuyu	East-Bantu	I	1.04	1	-1	37	1444	1.33	52670	2351512834	17.92	2.07	1.80	0.33	403.12
Ad41	Vugusu	East-Bantu	K	1.10	0	1	35	1868	2.27	72322	6707058434	20.57	1.64	2.61	0.54	709.76
Ad46	Soga	East-Bantu	N	0.61	1	1	33	1106	0.64	128027	14799781041	22.47	1.45	3.04	0.45	900.13
Ad47	Sumbwa	East-Bantu	N	0.63	1	-4	32	1167	0.75	126958	20139363151	21.23	1.65	1.72	0.75	783.54
Ad48	Toro	East-Bantu	N	0.90	0	1	31	1256	1.14	164579	14829464236	20.79	0.56	4.11	0.73	1102.29
Ad49	Zinza	East-Bantu	N	0.89	0	-3	31	1245	1.22	143991	18849962472	17.49	1.61	2.19	0.63	921.30
Ad50	Kaguru	East-Bantu	G	0.61	0	-6	37	886	3.10	99676	5888824305	20.30	4.78	2.35	0.33	196.30
Ad51	Ngulu	East-Bantu	K	0.43	0	-6	38	290	0.87	118774	4557872667	21.11	3.79	1.86	0.37	85.62
Ad7	Ganda	East-Bantu	K	0.50	1	1	32	1139	0.83	143340	15581893329	22.49	0.99	4.08	0.61	1000.31
Ad8	Hehe	East-Bantu	G	0.84	1	-8	35	1664	2.11	106154	13269084146	18.05	5.92	2.72	0.37	460.53
Ad9	Gisu	East-Bantu	I	0.61	0	1	34	1325	1.43	96256	10801510855	21.77	1.62	2.60	0.25	802.88
Ae12	Duala	Bantu-A-B10-B20-B30	K	0.41	0	4	10	148	1.05	205861	10244752778	24.24	0.33	1.81	0.63	22.80
Ae2	Kpe	Bantu-A-B10-B20-B30	K	0.60	0	4.2	9.3	261	2.30	212616	14404955165	24.95	0.34	1.71	0.56	24.27
Ae20	Ekonda	Central-Western-Bantu	K	0.18	0	-2	18	313	0.29	193130	9767982930	23.17	0.35	2.41	1.22	739.25

Ae28	Ngala	Central-Western-Bantu	G	0.06	0	1	18	325	0.15	188284	6321638490	22.94	0.27	2.67	1.08	896.57
Ae33	Ndaka	Ababuan	G	0.43	0	1	27	643	0.53	241762	6930236829	22.12	0.30	3.15	1.13	1495.40
Ae39	Ngombe	Central-Western-Bantu	K	-0.12	0	2	20	371	0.38	188204	7378565987	22.83	0.32	2.42	1.32	1121.19
Ae4	Nkundo	Central-Western-Bantu	I	-0.16	0	0	20	350	0.22	195206	6645956491	22.83	0.27	2.60	1.43	1042.80
Ae46	Mpongwe	Bantu-A-B10-B20-B30	I	0.22	0	-2	10	147	1.14	176543	11513687094	25.51	0.62	2.20	1.09	54.40
Ae48	Bafia	Bantu-A-B10-B20-B30	K	0.62	0	5	11	602	1.13	197487	12733258455	21.62	0.88	2.49	0.48	172.88
Ae5	Bamileke	Grassfields	I	0.63	0	5	10	550	2.98	202550	13678760552	22.49	0.77	2.85	1.27	102.55
Ae50	Bamun	Grassfields	G	0.45	0	6	11	834	1.57	187741	15731303961	20.75	1.36	2.94	0.63	252.80
Ae8	Rundi	East-Bantu	N	0.85	1	-3	30	1565	2.67	156814	20029282678	16.58	1.58	2.28	0.37	1028.06
Ah3	Tiv	Tivoid	N	-0.05	0	7	9	280	2.62	161827	13611477259	23.19	1.99	1.31	0.22	243.40

Environmental PCA

Data from 0.5 degree cells was extracted for all environmental variables from the region of Africa south of 9°N and east of 5°E. We used data on the mean and variance values for temperature, precipitation, and NPP, as well as elevation, for each 0.5 degree cell in a latitude/longitude-delimited region of Africa that includes the locations of all attested Bantu languages to derive independent composite variables representing environmental conditions in the region of Africa where Bantu ethnolinguistic groups are found (Fig S1). All Bantu societies are found in this region, and the early 20th century ecology of this region of Sub-Saharan Africa reflects the full spectrum of environmental conditions associated with the Bantu cultures in our sample. We use this data to derive independent environmental variables to represent these conditions using principal component analysis and to extract relevant values for sampled societies.

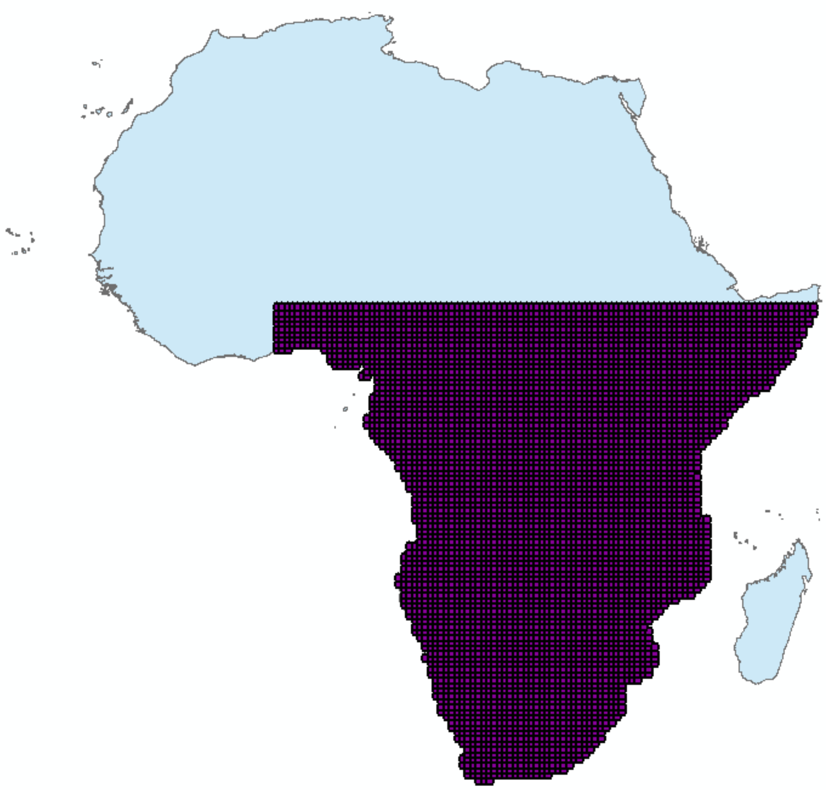

Figure S1: Environmental variables from 0.5 degree cells in the shaded region, including all of continental Africa south and east of 9°N, 5°E, were used in principal component analysis. n=5,005.

Based on eigenvalues, the first three components were selected as the best representation of variability in this data. Component loadings and cumulative variance are reported in Table S3. The first of these components is positively associated with mean NPP and mean precipitation, and negatively associated with temperature variance. The second component is negatively associated with mean temperature and positively associated with elevation. The third component is positively associated with precipitation variance and NPP variance.

Table S3: PCA on environmental variables from 0.5 degree cells across Sub-Saharan Africa. n = 5,005.

	PC1	PC2	PC3	Uniqueness
sqrt Mean NPP	**0.85**	0.20	0.26	0.18
Mean Precipitation	**0.81**	-0.11	0.44	0.13
log Temperature Variance	**-0.81**	0.46	0.03	0.13
Mean Temperature	-0.02	**-0.94**	-0.01	0.11
Elevation	-0.09	**0.87**	0.15	0.22
Precipitation Variance	0.17	0.13	**0.94**	0.07
sqrt NPP Variance	0.60	0.06	**0.68**	0.17
SS Loadings	2.43	1.92	1.63	
Cumulative Variance	0.35	0.62	0.85	

Reliance on agriculture

Because reliance on multiple different subsistence strategies creates dependencies in subsistence data and because Ethnographic Atlas subsistence data is binned in ways that prevent simple arithmetic combinations, we describe reliance on agriculture as a single, continuous metric derived from scalar information about reliance on plant agriculture, animal husbandry, fishing, hunting, and gathering.

Following Vilela et al (46), this variable is derived from the Ethnographic Atlas variables EA001 Subsistence economy: gathering, EA002 Subsistence economy: hunting, EA003 Subsistence economy: fishing, EA004 Subsistence economy: animal husbandry, and EA005 Subsistence economy: agriculture. Murdock (38) coded each of these variables as a range of percentages of dietary composition (0-5%, 6-15%, 16-25%, 26-35%, 36-45%, 56-65%, 66-75%, 76-85%, 86-100%). In order to account for the uncertainty created in the actual use of different subsistence strategies in this coding scheme, we generated 1000 possible combinations of exact percentage values while ensuring that these percentage values (i.e. the sum of dietary percentages across all subsistence sources) added to 100%. We summarized these values into unique variables using principal component analysis for compositional data in the *compositions* package for R. The first component in this analysis corresponds to increasing reliance on domesticated resources. We extracted scores for this first component for all societies in the sample as the variable 'reliance on agriculture'. See Vilela et al (46) for additional details on the construction of this variable.

D statistic of phylogenetic signal on full tree sample

We calculated the D statistic to measure phylogenetic signal in each land tenure norm on all 2,000 trees in the posterior sample. Distributions of D across the entire tree sample, as well as distributions of p-values for comparisons with 0 (consistent with the Brownian motion model of evolution) and 1 (consistent with random distribution of trait values) are provided in Figure S2.

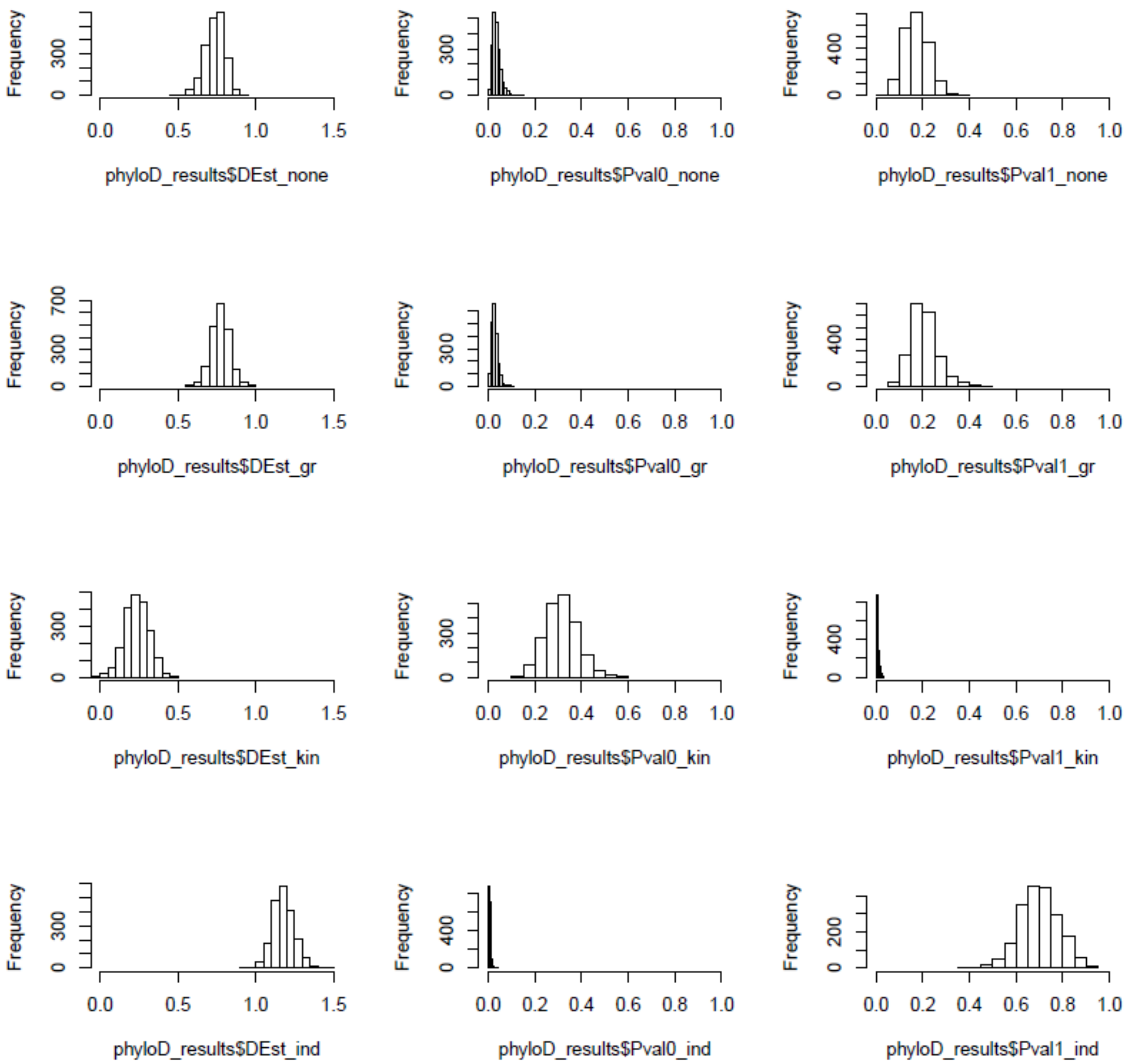

Figure S2: Phylogenetic signal measured by D-statistic on posterior tree sample (2,000 trees). X axis represents D-statistic. Y axis represents frequency.

D statistic of phylogenetic signal on geographic tree

A tree representing the geographic relationships between individual societies was constructed by applying unweighted pair group method with arithmetic mean (UPGMA) hierarchical clustering to the spatial distances between societies. The D statistic of phylogenetic signal was measured on this tree for each land tenure norm to measure the spatial clustering of each individual form of land ownership. The results of this analysis are reported in Table S3.

Table S4: Phylogenetic signal measured by D-statistic on geographic tree (from hierarchical clustering on lat/long coordinate distances)

LT Type	D-Statistic	p val 0	p val 1
Non	0.774	0.001	0.071
Group	0.842	<0.001	0.144
Kin	0.799	<0.001	0.094
Individual	1.125	<0.001	0.745

AIC comparison of evolutionary models

Additional information on the distribution of AIC values for alternative models of land tenure change are reported in Table X. ΔAIC is calculated based on the median AIC value for a particular model across the entire tree sample (n = 2,000).

Table S5: AIC comparison for alternative models of land ownership evolution

	Median AIC	Minimum AIC	Maximum AIC	ΔAIC
Alternative Unilinear	206.815	200.677	207.312	0.000
Loss For Change	207.312	201.102	207.312	0.497
Exclusivity Unilinear	207.312	203.400	207.312	0.497
Alternative Relaxed Unilinear	213.312	208.633	213.312	6.497
Exclusivity Relaxed Unilinear	213.312	210.252	213.312	6.497
Alternative Rectilinear	214.197	203.457	227.413	7.382
Unstable Group	215.312	215.312	215.312	8.497
Full	219.312	219.312	219.312	12.497
Kin-Group	221.369	212.287	229.990	14.554
No Loss	221.471	213.944	231.072	14.656
Corporate	230.409	221.704	240.472	23.594
Rectilinear	233.003	217.748	248.653	26.188
Gain From None	258.135	242.313	278.265	51.320

AIC comparison of macroecological models

Table S6: Support for alternative models of land ownership, coded as binary (presence/absence of any land ownership available to a majority of the society's population; absence of ownership for a majority of community members treated as reference level). n = 65 societies.

Model	AICc	ΔAICc	AICw
Neighbor Effect + Productivity Uncertainty	58.41	0.00	0.09
Neighbor Effect	59.63	1.22	0.05
Neighbor Effect + Distance to Coast	59.82	1.42	0.05
Neighbor Effect + Productivity Uncertainty + Reliance on Agriculture	59.82	1.42	0.05
Neighbor Effect + Reliance on Agriculture	59.89	1.49	0.04
Neighbor Effect + Productivity Uncertainty + Intensive Agriculture	59.97	1.56	0.04
Neighbor Effect + Productivity Uncertainty + Productivity	60.12	1.71	0.04
Neighbor Effect + Reliance on Agriculture + Intensive Agriculture	60.59	2.18	0.03
Neighbor Effect + Productivity Uncertainty + Mountains	60.59	2.19	0.03
Neighbor Effect + Intensive Agriculture	60.62	2.21	0.03
Neighbor Effect + Productivity Uncertainty + Distance to Coast	60.64	2.24	0.03

Table S7: Multi-model average for models of land ownership in agricultural societies (full average) excluding five societies that did not rely on agriculture for the majority of their subsistence (see Methods for details) (n = 60). Intensive agriculture coded as binary (presence/absence of intensive agriculture; absence of intensive agriculture treated as reference level). Land ownership coded as binary (presence/absence of any land ownership available to a majority of the society's population; absence of ownership for most community members treated as reference level). Standardized coefficients are presented.

Parameter	β coefficient	Standard error	z value	RVI
(Intercept)	-2.963	1.427	2.034	1.00
Neighbor Effect	8.150	2.322	3.433	1.00
Productivity	0.064	0.175	0.360	0.36
Productivity Uncertainty	-0.064	0.218	0.290	0.34
Mountains	0.007	0.115	0.117	0.29
Intensive Agriculture	-0.152	0.561	0.265	0.26
Distance to Coast	-0.002	0.236	0.007	0.23
Reliance on Agriculture	0.010	0.493	0.019	0.23

Marginal $R^2_{GLMM} = 0.51$, and conditional $R^2_{GLMM} = 0.60$

Table S8: Support for alternative models of land ownership, coded as binary (presence/absence of any land ownership available to a majority of the society's population; absence of ownership for a majority of community members treated as reference level). Sample excludes five societies that did not rely on agriculture for the majority of their subsistence (see Methods for details) (n = 60).

Model	AICc	ΔAICc	AICw
Neighbor Effect	52.22	0.00	0.12
Neighbor Effect + Productivity	53.32	1.10	0.07

Neighbor Effect + Mountains	53.40	1.18	0.07
Neighbor Effect + Productivity Uncertainty	53.41	1.20	0.07
Neighbor Effect + Intensive Agriculture	54.02	1.80	0.05
Neighbor Effect + Productivity Uncertainty + Productivity	54.12	1.90	0.05
Neighbor Effect + Distance to Coast	54.34	2.12	0.04
Neighbor Effect + Reliance on Agriculture	54.52	2.30	0.04
Neighbor Effect + Mountains + Productivity	55.29	3.07	0.03
Neighbor Effect + Intensive Agriculture + Productivity	55.44	3.22	0.02