Gavin Michael C. (Orcid ID: 0000-0002-2169-4668)

Title: The Biogeography and Evolution of Land Ownership

Running Title: Biogeography of Land Ownership

Hannah J. Haynie[1], Geoff Kushnick[2], Patrick H. Kavanagh[3], Carol R Ember[4], Claire Bowern[5], Bobbi S. Low[6], Ty Tuff[7], Bruno Vilela[8], Kathryn R. Kirby[9,10], Carlos A. Botero[11], and Michael C. Gavin[3,9*]

[1]Department of Linguistics, University of Colorado, Boulder, CO, USA
[2]School of Archaeology and Anthropology, Australian National University, Canberra, ACT, Australia
[3]Department of Human Dimensions of Natural Resources, Colorado State University, Fort Collins, CO, USA
[4]Human Relations Area Files, Yale University, New Haven, CT, USA
[5]Department of Linguistics, Yale University, New Haven, CT, USA
[6]School for Environment and Sustainability, University of Michigan, Ann Arbor, MI, USA
[7]Environmental Data Science Innovation and Inclusion Lab (EESIL) NSF Synthesis Center and Earth Lab, CIRES, University of Colorado, Boulder, CO, USA
[8]Institute of Biology, Universidade Federal da Bahia, Salvador, BA, Brazil
[9]Department of Linguistic and Cultural Evolution, Max Planck Institute for The Science of Human History, Jena, Germany
[10]Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, Canada
[11]Department of Integrative Biology, University of Texas, Austin, TX, USA

* Corresponding author email: michael.gavin@colostate.edu

Conflict of Interest Statement
All authors declare that they have no conflicts of interest.

Abstract
Aim
Land ownership norms are well-documented and play a central role in social-ecological systems. Yet only recently has the spatial and temporal distribution of land ownership been examined using biogeographical and evolutionary approaches. We incorporate biogeographical and evolutionary modelling to test associations between land ownership and environmental, subsistence, and cultural contact predictors.

Location
Africa.

Taxon
Bantu and Bantoid ethnolinguistic groups (73 societies).

Methods
Based on ethnographies for 73 societies, we coded land ownership norms as none, group, kin, or individual. We paired these data with language phylogenies, and measured phylogenetic and geographic signal and modeled alternative evolutionary trajectories using maximum likelihood methods. We tested the influence of environmental, subsistence, and cultural predictors on spatial variation in land ownership, using a multi-model inference approach based on logistic regression.

Result

Bantu land ownership norms likely evolved on a unilinear trajectory (i.e. societies progress or regress along a series of ownership types), but not one requiring consistent increase in exclusivity (i.e. restrictions toward ownership by smaller groups) as suggested by prior theory. Our biogeographical analyses suggest land ownership is more likely where neighbors also own land and resource productivity is predictable. Reliance on agriculture has relatively small effect sizes and low importance in the model.

Main Conclusions

We find support for multiple evolutionary pathways. Lack of resolution may be due to localized horizontal transfer of norms consistent with the influence of neighbors we find from biogeographical analyses. We cannot rule out other untested mechanisms. Although long-standing theories propose links between subsistence practices and land ownership, our results suggest subsistence plays only a modest role. Our results also support resource defensibility theory (i.e., land ownership is more likely where environmental productivity is predictable). Overall, we demonstrate the value of combining analytical approaches from evolution and biogeography to test hypotheses on the spatial and temporal variation of human cultural traits.

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 cultural traits. Land tenure has been studied extensively from cultural, political, economic, and natural resource management perspectives (Ember, Adem, Brougham, & Pitek, 2021; Feder & Feeny, 1991; Mackenzie, 2003; Peters, 2009; Platteau, 1996; Robinson, Holland, & Naughton-Treves, 2014), and theories on property rights date back centuries (Hobbes, 1651; Hume, 1739; Locke, 1690). The biogeographical and evolutionary 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 biogeographical and evolutionary analyses to test hypotheses regarding temporal and spatial patterns in land ownership norms in a sample of Bantu societies.

There are two main components to our study. The first is to explore and compare different models of evolutionary change over time. The research questions here are: 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? Although there are many possible combinations of our four types of land tenure (none, group, kin, or individual), we focus on a smaller set of models that have been discussed in the literature. The second component is to test three prominent hypotheses regarding the factors that may shape the spatial patterns of land ownership. Land ownership norms not only vary over time, but also across space (see Figure 1).

For our first component (C1) we use phylogenetic methods adopted from evolutionary biology to compare different hypothetical evolutionary trajectories of land ownership. 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? One hypothesis (C1.H1) advanced by early theorists argues for rectilinear trajectories, in which societies progressed in one direction through a series of four theoretically established stages of land tenure linked to subsistence approaches (e.g. de Laveleye, 1874; Morgan, 1877). 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 a strict rectilinear model (Carneiro, 2003; Currie, Greenhill, Gray, Hasegawa, & Mace, 2010; Currie & Mace, 2011; Sanderson, 2007). One alternative (C1.H2) is a unilinear trajectory in which societies may progress or regress along the same series of four land ownership types (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 (Brown & Podolefsky, 1976; Kavanagh et al., 2020; Netting, 1993; Smith, 1988). Although less explored, we can also test the hypothesis (C1.H3) that other trajectories may also be possible in which land ownership change is not restricted to shifts up and down the N-G-K-I scale, but rather any form of ownership can change into any other form if conditions are suitable (see Fig 2a; Kushnick, Gray, & Jordan, F. M. 2014). Details of the models can be found in section **2.2.**

Land ownership norms not only vary over time, but also across space (see Figure 1). Long-standing debates spanning multiple academic disciplines, including ecology, economics, and anthropology, still exist regarding which factors shape spatial patterns in land ownership (Acheson et al., 2015; Chabot-Hanowell & Smith, 2012; Dyson-Hudson & Smith, 1978; Ember et al., 2021; Kavanagh et al., 2020). For

our second component (C2), we use a multi-model inference approach to test three prominent general hypotheses regarding the factors that shape the spatial patterns of land ownership.

C2.H4: Cultural norms will be shaped by both vertical (i.e. culture being passed from one generation to the next, such as from parents to children) and horizontal (i.e. culture being passed within the same generation, such as from one neighbor to another) cultural transmission. H4a: If vertical transmission is prominent, we predict that closely related societies will have similar land ownership norms. H4b: If horizontal transmission plays a major role, we predict that societies that are in closer contact (e.g., neighboring groups) should have similar ownership norms.

Research on territoriality by ecologists, anthropologists, and economists has converged on the theory of resource defensibility, which argues that land ownership is more likely where environmental productivity is predictable (Anderson & Swimmer, 1997; Baker, 2003; J. L. Brown, 1964; Demsetz, 1967; Dyson-Hudson & Smith, 1978; Lueck, 1994; Maynard Smith, 1982). Other researchers have found evidence to support defensibility theory to explain variation in property systems (e.g., Acheson et al, 2015; Ember et al., 2021). One of the parameters of defensibility theory is whether land has predictable value that is worth defending. Another, which may help explain why land ownership might be private or communal, is whether an individual can defend the resource or needs help from a group. Defensibility theory also leads us to hypothesize:

C2.H5: As the density and predictability of resources increases so too do the benefits of defending these resources, which should lead to a greater probability of individuals or groups owning land (Acheson et al., 2015; Chabot-Hanowell & Smith, 2012; Ember et al., 2021; Kavanagh et al., 2020; Rose, 1998).

Land ownership norms may also be shaped by the subsistence strategies prevalent in a society. Prior theory suggests that the absence of property rights can prove to be a barrier to the development of agricultural practices (Bowles & Choi, 2013; Endicott, 1988; Woodburn, 1982). The use of agriculture, as well as increasing intensification of agricultural practices, require substantial labor inputs, which may only be worth pursuing if the benefits of the harvest can be ensured through property rights (Bowles & Choi, 2013; Woodburn, 1982). Similarly, the costs of establishing and enforcing property rights may not be worth taking on if the resources the land produces are limited or diffuse (Dyson-Hudson & Smith, 1978). The development of agriculture, and increasing intensification of agriculture, may increase the amount of resources land can produce per unit area, making it worth the effort to establish and maintain property rights (Bowles & Choi, 2013; Dyson-Hudson & Smith, 1978). Based on these theoretical links between subsistence strategies and land ownership norms, we hypothesize:

C2.H6: Certain subsistence strategies will be associated with specific land ownership norms. For example, here we test H6a: Agriculture will be associated with private land tenure (Bowles & Choi, 2013); and H6b: Intensification of agriculture is linked with land ownership (P. Brown & Podolefsky, 1976). We 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) (see Methods for details on how each factor is measured).

We focus our analysis on the temporal and spatial variation in land ownership of Bantu-speaking societies for three main reasons. First, 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. Dobson, 1954; Kajoba, 2002; Mugerwa, 1966; Shipton, 1984). Second, the historical relationships among Bantu societies are well-characterized by a language phylogeny (Grollemund et al., 2015), making it possible to implement phylogenetic analysis of trait evolution (Mace et al., 1994). Third, 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

Dependent variable: We included land ownership norms coded for 73 societies that are included in the reference phylogeny for Bantu (Grollemund et al., 2015), and for which Ethnographic Atlas data and environmental variables are available through the D-PLACE database (Colwell, 1974; Danielson & Gesch, 2011; Gray, 1999; Kirby et al., 2016; Lima-Ribeiro et al., 2015; Murdock, 1967; Running, Ramakrishna, Glassy, & Thornton, 1999) (See supplementary material for full dataset, Tables S1 and S2). This constitutes the largest sample of Bantu-speaking societies for which both phylogenetic and cultural information are available. We coded land tenure data based on ethnographic descriptions of each society (see supplementary materials). Following Kushnick et al. (2014), we coded each society's primary land ownership norm as one of four theoretically motivated categories: 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 (Cotula, 2007). 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. (2014) 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.

Independent variables: As we outlined in the introduction section, we test three sets of factors hypothesized (H4-H5) to shape the spatial patterns of land ownership: cultural transmission mechanisms (i.e. horizontal and vertical transmission), density and predictability of resources, and subsistence strategies. 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 (Kavanagh et al., 2020). To test for the effects of vertical cultural transmission, we included language classification information from Glottolog 4.0 (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; Hammarström et al., 2019).

We included environmental variables that have proposed to influence resource density and variability, and for which we have data available via D-PLACE (Kirby et al., 2016). Higher temperatures and more precipitation, as well as greater net primary productivity (NPP) may be associated with greater resource density (Gavin et al., 2018; Kavanagh et al., 2018). Variables describing the annual mean and variance for temperature (°C) and precipitation (mm) are from the Baseline Historical (1900–1949) CCSM ecoClimate model (spatial resolution of 0.5°; (Lima-Ribeiro et al., 2015)). Monthly net primary productivity (NPP, measured in kgC/m^2) reflect annual mean and variance from data obtained from the MODIS dataset (spatial resolution of 1 km; Running et al., 1999). Each of these variables was extracted for the latitude and longitude coordinates assigned to each society in D-PLACE; some of these coordinates are rounded to integer degrees, placing them at arbitrary points in the ranges of these societies rather than centroids of ethnolinguistic ranges. To avoid problems of multicollinearity among these different temperature, precipitation, and NPP variables we derived a set of independent environmental variables using principal component analysis (see supplementary materials, Fig S1). We used three components from this PCA in our final models (Table S3). The first of these components we refer to as environmental productivity, and it is positively associated with mean NPP and mean precipitation, and negatively associated with temperature variance. The second component we call mountainous, and it is negatively associated with mean temperature and positively associated with elevation. The third component we named productivity uncertainty, and it is positively associated with precipitation variance and NPP variance.

In addition to the three principal components listed above, we also explored the effects of two other environmental variables: elevation and distance to coast. More mountainous regions tend to have patchy resources, which can lead to competition for valuable locations (Cashdan et al., 1983). Therefore, mountainous regions may favor land ownership, because the benefits of defending resources may outweigh the costs, as argued by resource defensibility theory (Kavanagh et al., 2020). Locations closer to coasts may also have higher densities of available resources due to access to marine ecosystems (Hassan, F. A., 1975; Kavanagh et al., 2018). We gathered data on elevation (m) and distance to coast (km) in D-PLACE from the Global Multi-resolution Terrain Elevation Data of the U.S. Geological Survey (U.S. Geological Survey, 2010).

To test the effects of subsistence, we included a variable that characterizes each society's dietary reliance on specific subsistence activities. Following Vilela et al (2020), we derived this variable via a principal component analysis on Ethnographic Atlas variables (see supplementary materials for details). We also included a measure of agricultural intensity by recoding variable EA 028 from the Ethnographic Atlas (Kirby et al., 2016; Murdock, 1967) as a binary variable, representing the presence or absence of intensive agriculture. We used variance inflation factors to measure for any multicollinearity between the measure of dietary reliance and the measure of intensive agriculture because redundancy in the characterization of subsistence could theoretically interfere with the identification of meaningful effects.
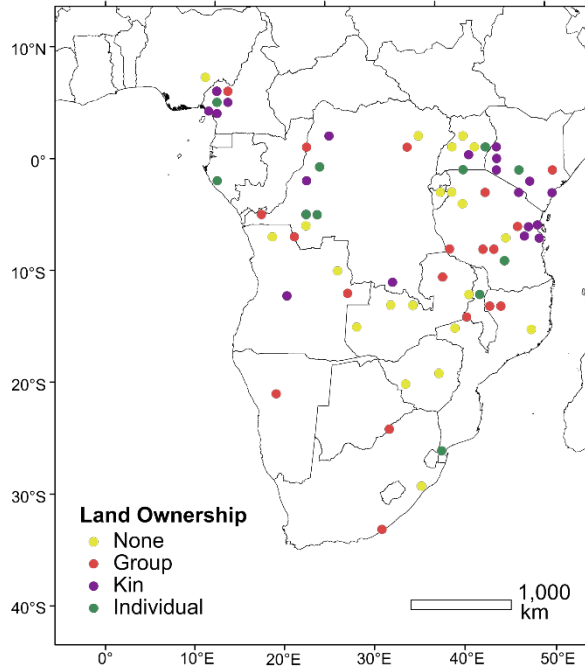
[one column width] *Figure 1: Land tenure norms associated with a majority of the population for Bantu and Bantoid ethnolinguistic groups of Africa (n= 73). Map uses an Aitoff equal area projection.*

2.2 Phylogenetic analyses of evolution of land ownership (Component 1)

We characterized the evolution of land ownership by measuring phylogenetic (δ) and geographic signal in the land ownership norms data, and modeling alternative evolutionary trajectories using maximum likelihood parameter estimation in a continuous time Markov chain model of multistate trait evolution. These analyses paired land tenure data described above with Bantu language trees produced by Grollemund et al. (2015). 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 (Grollemund et al., 2015) 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 (Bouckaert et al., 2014). Because this tree faithfully represents the information in the full tree sample (see Fig S1), 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 δ statistic for binary characters (Borges et al., 2019). This statistic uses the concept of Shannon entropy to estimate the level of phylogenetic signal between a categorical trait and a phylogeny. δ increases with increasing strength of phylogenetic signal, and the significance of a δ estimate can be evaluated by simulating a p-value through a permutation test. We estimated the δ statistic and associated p-value for our land tenure trait on the Bantu MCC tree using the *ape* package for *R* (Paradis & Schliep, 2019) and procedures outlined by Borges et al. (2019). To evaluate whether similarities in land ownership are structured spatially we calculated the assortativity of our land tenure trait (Newman 2002) on a Gabriel neighbor graph (Gabriel & Sokal, 1969) derived from the spatial coordinates of the Bantu societies in our sample (Fig S2). Assortativity ranges from -1, which represents the dispersal of perfect disassortativity, to 1, which

represents the tight clustering of trait values associated with perfect assortativity. An assortativity value of 0 indicates neutral assortativity, or unstructured variation of trait values on the neighbor graph. We used the *graph4lg* package for *R* to construct the Gabriel neighbor graph (Savary et al., 2020) and the *igraph* package for *R* to calculate assortativity of our land tenure trait on this graph (Csardi & Nepusz, 2006).

We used the *MultiState* phylogenetic comparative method of the *BayesTraits V3* software package to evaluate possible evolutionary trajectories for land ownership norms (Pagel, 1999; Pagel, Meade, & Barker, 2004). 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, theoretically motivated 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 theoretically motivated candidate models of land ownership trait evolution as Kushnick et al. (2014). 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. The 12 models we test in addition to the full model are motivated by prior research and can be broadly grouped into four categories (progressive gain of exclusivity, progressive alternative trajectory, restricted reversion to non-ownership or less exclusive norms, and models that focus on a private ownership distinction), each of which are implemented in three different variations. For progressive models, two trajectories were evaluated: one which orders states according to the level of exclusivity in ownership (*Exclusivity Gain*, N-G-K-I), and an alternative supported by Kushnick et al. 2014 that places individual ownership between non-ownership and group ownership (*Alternative*, N-I-G-K) were explored. Progressive models are implemented in three variations: *Rectilinear* (sequential changes in a single direction), *Unilinear* (sequential changes in either direction), and *Relaxed Unilinear* (sequential changes in either direction, plus transitions from any state to N). One set of non-progressive models centers on whether and how reversion to non-ownership or less exclusive ownership norms may happen. 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. A final set of models focuses broadly on distinctions between ownership and non-ownership or private vs. non-private ownership. 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 (Component 2)

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

cultural transmission mechanisms, density and predictability of resources, and subsistence strategies 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 (Burnham & Anderson, 2002; Kavanagh et al., 2020). For this analysis we recoded land ownership as a binary variable (0 = no ownership; 1 = group, kin, or individual ownership).

We centered (by subtracting mean) and scaled (by standard deviation) all continuous variables included in the model. We included language classification as a random effect to account for shared ancestry (Botero et al., 2014; Gavin et al., 2018; Hammarström, Forkel, & Haspelmath, 2019). 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 multi-model inference (Burnham & Anderson, 2002) 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* (Bartoń, 2020). We implemented model averaging based on AIC weights to account for uncertainty across multiple competing models. The AICw of the best model is 0.09 (see Table S4 in supplementary materials), suggesting that model averaging is an appropriate method for this study (Burnham & Anderson, 2002). We used Moran's I to test for spatial autocorrelation in model residuals.

One of our subsistence strategy variables, the measure of intensive agriculture, focused solely on agricultural practices. Therefore, we also ran our multimodel inference analysis with a sample that excluded 5 societies (n = 60), which are generally considered non-agriculturalists (i.e. Mbuti and Herero) or rely on agriculture for less than 50% of their subsistence (based on the Ethnographic Atlas variable EA005; Kirby et al., 2016; Murdock, 1967: Lozi, Sangu, and Ngala).

3. Results

3.1 Evolutionary trajectories of land ownership (Component 1)

The δ statistic value four our categorical land ownership trait (δ = 0.156) demonstrates a level of phylogenetic signal on the Bantu MCC tree that is significantly higher than what we would expect by chance (p = 0.02), suggesting that land tenure in Bantu societies does show some phylogenetic signal. In contrast, we find an assortativity measure for the land ownership variable on a Gabriel network graph of Bantu societies derived from their spatial coordinates of 0.062. Because this assortativity measure is close to 0, we infer that the spatial variation in this trait is not highly structured (see Discussion section for additional details).

Based on AIC evidence, we find that the Alternative Unilinear model (an alternative form of the unilinear hypothesis (H2)) best fits the patterns we see in land ownership in Bantu-speaking societies (Fig. 2b). We also find some support for another version of the unilinear hypothesis (H2), 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. We also found evidence supporting another trajectory (H3) that was neither rectilinear, nor some version of unilinear. 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, including the rectilinear model (H1) are not supported by our results (ΔAIC >2).

[full page width] *Figure 2: a) Models of land ownership change considered in phylogenetic analysis; b) Comparison of AIC values for alternative models on 2,000 tree posterior sample for 73 Bantu and Bantoid ethnolinguistic taxa of Africa. Red box indicates, for each model, interquartile range (IQR) of AIC values. Black line through box represents median AIC.*

3.2 Drivers of spatial variation in land ownership (Component 2)

H4 predicts that vertical and horizontal transmission will be important. Neighbor effect (proportion of neighboring societies with private ownership) is an important predictor of land ownership in this sample, occurring in all models with $\Delta AIC < 2$. The relatively large multimodel average effect size for this variable (Table 1) suggests that the land ownership practices of neighboring societies (our proxy for horizontal transmission) are important for predicting land ownership norms. 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 (our proxy for vertical transmission) does not account for a large proportion of the variation in land ownership.

H5 predicts that land ownership might be more likely to occur where resource productivity is predictable and this appears to be supported. Productivity uncertainty occurs in several models with $\Delta AIC < 2$ 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.

Regarding H6, while we may have expected that agriculture, and in particular intensive agriculture, should be an important predictor of land ownership (Brown & Podolefsky, 1976), we find that reliance on agriculture and intensive agriculture are associated with relatively small effect sizes and relatively low importance in the averaged model. We found no issues with multicollinearity between the different measures of subsistence strategies (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 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 in Bantu societies (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
Mountainous	-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. In our tests of different hypothesized evolutionary trajectories, we find support for three possible models: the Alternative Unilinear model and the Exclusivity Gain Unilinear model, which each allow transitions in both directions along a fixed trajectory, and the Loss for Change model (Figure 2a) which does not allow transitions between G, K, and I. Contrary to expectations that ownership should evolve along a trajectory of increasing exclusivity of rights (cf. de Laveleye, 1874; Kushnick et al., 2014; Morgan, 1877; Smith, 1988), which is referred to as the rectilinear model (C1.H1), we find evidence for trajectories in which individual ownership may follow non-ownership (i.e. both Alternative Unilinear and Loss for Change). Our results are similar to those for Austronesian societies reported in the only other phylogenetic-based analysis of land ownership to date (Kushnick et al., 2014). That we find evidence for this alternative pathway in a second major ethnolinguistic family suggests that the development of individual ownership 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.

In our tests of the prominent hypotheses regarding the factors that shape spatial patterns of land ownership, we found that proportion of neighboring societies with private ownership (H4b) and productivity uncertainty (H5) are both important predictors. 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 clustered in space, 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.

Early tests of resource defensibility theory, based largely on qualitative case studies or limited sample sizes, produced mixed results (Baker, 2003; Cashdan et al., 1983; Dyson-Hudson & Smith, 1978). More recently, Ember et al. (2021) and Kavanagh et al. (2020) 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 (2015) 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 (Dyson-Hudson & Smith, 1978; Ember et al., 2021; Kavanagh et al., 2020). Private ownership of land may facilitate the

defense of natural resources in environments where those resources are reliable enough to justify such actions.

One longstanding idea focuses on the relationship between land ownership and subsistence practices (Boserup, 1965; Bowles & Choi, 2013; P. Brown & Podolefsky, 1976; Otsuka & Place, 2015). 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 (H6). However, reliance on agriculture (H6a) and intensive agriculture (H6b) play only a modest role compared with other 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 (Fallers, 1955; Kajoba, 2002; Mugerwa, 1966). 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 (Dobson, 1954). 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 (Smith et al., 2010). 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.

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. Our results also demonstrate the value of integrating analytical approaches from the fields of evolution and biogeography in order to produce new insights into the drivers of spatial and temporal trends in land ownership. We argue that similar approaches can be used in future studies to test theories about the spatiotemporal variation of other human cultural traits.

Data Availability
All data are available from www.d-place.org and https://doi.org/10.5061/dryad.zs7h44jf0. Ethnographic variables are secondary data collected from published ethnographies, and are now all open access and available to the studied populations.

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Biosketch

The research team is an international, interdisciplinary group of ecologists, evolutionary biologists, geographers, linguists, and anthropologists, which grew out of initial efforts to construct the Database on Places, Language, Culture and Environment (www.d-place.org) that empowers investigations on the geography and evolution of human cultural diversity. All authors contributed to idea conception and writing, HJH, MCG, and GK collected the data, HJH analyzed the data, HJH and MCG led the writing.

Land Ownership
- None
- Group
- Kin
- Individual

1,000 km

a.

Full

N ↔ G

I ↔ K

Exclusivity Gain

Rectilinear
N → G
I ← K

Unilinear
N ↔ G
I ↔ K

Relaxed Unilinear
N → G
I ↔ K

Alternative

Rectilinear
N → G
I → K

Unilinear
N ↔ G
I ↔ K

Relaxed Unilinear
N ← G
I ↔ K

No Loss
N ↔ G
I ↔ K

Loss for Change
N ↔ G
I   K

Gain from None
N → G
I   K

Unstable Group
N → G
I ↔ K

Kin-Group
N ↔ G
I → K

Corporate
N → G
I ↔ K

b.

MODEL