

## Drivers of global variation in land ownership

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### Abstract

Land ownership shapes natural resource management and social-ecological resilience, but the factors determining ownership norms in human societies remain unclear. Here we conduct a global empirical test of long-standing theories from ecology, economics, and anthropology regarding potential drivers of land ownership and territoriality. Prior theory suggests that resource defensibility, subsistence strategies, population pressure, political complexity, and cultural transmission mechanisms may all influence land ownership. We applied multi-model inference procedures based on logistic regression to cultural and environmental data from 102 societies, 71 with some form of land ownership and 31 with no land ownership. We found an increased probability of land ownership in mountainous environments, where patchy resources may be more cost effective to defend via ownership. We also uncovered support for the role of population pressure, with a greater probability of land ownership in societies living at higher population densities. Our results also show more land ownership when neighboring societies also practiced ownership. We found less support for variables associated with subsistence strategies and political complexity.

### Keywords

Human biogeography, cultural transmission, land ownership, resource defensibility, subsistence

## Introduction

Land ownership systems determine who can access and exploit resources in a particular area, and who can expect to inherit those resources over the long term. As such, land ownership is a cultural trait that plays a critical role in shaping natural resource management practices and influences the resilience of social-ecological systems (Hardin 1968, Ostrom et al. 1999, Costanza et al. 2001). However, not all human societies practice land ownership (e.g., Figure 1). Despite major advances in our understanding of the social and ecological outcomes of different ownership systems, it remains unclear what factors determine which societies maintain some form of land ownership and which have no land ownership. In recent years, a growing number of studies have applied theoretical and methodological advances in biogeography and macroecology to contribute to long-standing debates regarding the geographical distributions of human diversity (e.g., Harcourt 2012, Botero et al. 2014, Freeman and Anderies 2015, Gavin et al. 2018, Kavanagh et al. 2018, Pacheco Coelho et al. 2019). Here we apply analytical approaches developed in the field of biogeography to provide a global empirical test of hypotheses developed in multiple academic disciplines regarding geographic patterns of land ownership.

The foundations of property rights theory dates back to the 17<sup>th</sup> century (e.g., Hobbes 1651, Locke 1690, Hume 1739). A central question over this long history of investigation has been what factors lead to the adoption of different land ownership systems (e.g., Ember et al. In press, Rudmin 1992, Acheson et al. 2015). Overall, previous research and theory point to a limited set of factors as possible drivers of land tenure systems: resource defensibility, subsistence strategies, population pressure, political complexity, and cultural transmission mechanisms.

Over the course of the 20<sup>th</sup> century work in ecology, economics, and anthropology has converged on the theory that the density and predictability of focal resources shape the benefits and costs of defending the resources, and in turn determine land ownership (Rose 1998, Chabot-Hanowell and Smith 2012, Acheson

et al. 2015). For example, in ecology, work on territoriality (e.g., Brown 1964) and game theory (e.g., Maynard Smith 1982) has noted that species will defend territories only if the action provides a net fitness gain. Similarly, in economics, Demsetz (1967) and others (e.g., Lueck 1994, Anderson and Swimmer 1997, Baker 2003) developed the cost-benefit theory from the early foundations built by Locke, Hobbes, and Hume. Anthropologists have applied these ideas, which some call economic defensibility theory (Dyson-Hudson and Smith 1978), to explain territoriality in hunter-gatherer societies.

Resource defensibility theory predicts that as resource density and predictability increase, individuals or groups should exert more control over land. However, when resource density and predictability decrease, the probability of some form of land ownership should also decrease (Chabot-Hanowell and Smith 2012). Others suggest that in highly unpredictable environments communal land ownership may provide a buffer against unexpected hazards (e.g., Winterhalder 1990, Berry 2002, Peters 2004). Empirical tests of the resource defensibility theory have produced mixed results, with some support found (e.g., Dyson-Hudson and Smith 1978, Baker 2003, Chabot-Hanowell and Smith 2012), but also some contradictions (e.g., Cashdan et al. 1983). Importantly, the tests of the theory to date have been mostly limited to qualitative case studies (e.g., Dyson-Hudson and Smith 1978), limited sample sizes (e.g., Cashdan et al. (1983) 4 societies; Baker (2003) 14 societies), and mostly applied to hunter-gatherer groups (Chabot-Hanowell and Smith 2012). Recently, Ember et al. (in press) also found support for resource defensibility as a driver of private versus communal land tenure. However, in a global analysis focused only on hunter-gatherer societies, Freeman and Anderies (2015) found societies were more likely to recognize some form of land ownership when resources became less predictable and less dense.

Changes in land ownership have also been linked to changes in subsistence strategies. For example, the adoption of agriculture in the early Holocene may have coincided with the development of private property (Bowles and Choi 2013). In more recent times, arid and semi-arid rangelands characterized by

high variability in precipitation and primary productivity lend themselves to the transhumance responses of pastoralists (Ellis and Galvin 1994, Fratkin and Roth 2006, McPeak et al. 2011). Communal land ownership facilitates this movement, and avoids overexploitation of localized resources (Charnley 1997, Nugent and Sanchez 1999). In turn, changes in both technology and environment may drive changes in land ownership regimes.

Growing populations and increasing population density place pressure on available resources and this may also influence the sustainability of a society (Hardin 1968). Increasing population pressure creates competition for resources, including land; and some hypothesize that this challenge may be alleviated by recognized land ownership norms (Boserup 1965, Hardin 1968, Guillet 1981, Rosenberg 1990). In the case of foraging societies, increased population pressure may result in territoriality or group ownership of land (Dyson-Hudson and Smith 1978, Rosenberg 1990), while in societies practicing agriculture it may lead to increased levels of privatization of land (Boserup 1965, Hardin 1968).

Prior research has also emphasized the importance of social conditions needed to secure different forms of ownership (e.g., social norms, rules, regulations, laws) (Smith 1988, Krier 2009). In all cases where some form of recognized land ownership occurs, some kind of enforcement of these norms is required and political complexity may reduce the costs of enforcing land ownership. Anthropologists have used archaeological and ethnographic data to categorize the organization of human groups into a range of different forms that vary in their level of complexity (Murdock 1967, Currie et al. 2010). Bands and tribes tend to be more egalitarian in their political structures. Chiefdoms involve collections of local groups overseen by a centralized, and often hereditary, leadership. States comprise even more centralized leadership with the presence of specialized administrative roles and increased political bureaucracy. Higher levels of political complexity may ensure that the rules and regulations needed to maintain stricter forms of land tenure can be created and enforced across a large population.

The choice of land tenure system may also be affected by the sharing of information across generations and between cultural groups. In turn, we might predict that a society would be more likely to adopt land tenure strategies that are similar to their immediate ancestors (i.e. vertical transmission). Also, societies might be more likely to use land tenure systems similar to other societies in the same region with whom they have more regular contact (i.e. diffusion via horizontal transmission).

Here we compare the relative predictive power of all these factors - resource density and predictability, subsistence strategies, population pressure, political complexity, and cultural transmission mechanisms - across a global set of societies.

## Methods

All data used for our analyses are freely available via the D-PLACE database ([www.d-place.org](http://www.d-place.org); Kirby et al. 2016) or are in the supplementary table. Multiple systems of categorizing land tenure have been proposed (e.g., De Laveleye 1891, Smith 1988, Netting 1993, Kushnick et al. 2014). In this study, the main land ownership norm (i.e. the land ownership norm associated with the majority of people in a society at the time of ethnographic description) was coded for 102 societies from ethnographic descriptions in eHRAF World Cultures (<http://ehrafworldcultures.yale.edu/>, see supplementary table 1).

The data we used on land tenure were collected at a specific point in time for each society. We only used those collected at points that fell within a relatively narrow time span (1800-1965) in order to restrict any effects of the long-term dynamics of environmental and social conditions, including changes to what group occupied a given location over the course of history. We also recognize that the societies in our database all have unique histories, including distinct impacts due to the expansion of colonial regimes and national governments, that cannot be fully accounted for with any set of possible independent variables.

Based on a pilot study of 50 societies, eHRAF OCM identifiers 423 (Real Property) and 428 (Inheritance)

were identified as the categories of ethnographic description associated with a majority of land ownership information. Passages associated with these eHRAF identifiers were considered for all 102 societies described adequately in both eHRAF and D-PLACE (Kirby et al. 2016). Land ownership norms were coded as belonging to one of two categories (following Kushnick et al. 2014): no recognized ownership of land ('none'; e.g., groups that see land as a free good, such as the Agta of the Philippines (Headland and Headland 1993); total was 31 societies), or some ownership (which included any form of group ownership (i.e., land held by groups of related or unrelated individuals that may include what might be termed common-pool ownership, or ownership by individuals; total was 71 societies). Land tenure norms for all societies in this sample were coded by at least two coders. Inter-coder reliability for the independent categorization of land tenure norms as non-ownership versus some ownership of land across all societies in the sample was 89%. Cases involving coder disagreement were revisited by the team of coders periodically throughout the coding process to reconcile differences via negotiated agreement (Garrison et al. 2006, Campbell et al. 2013), resulting in full resolution of all coding disagreements through discussion (100% agreement).

We selected a series of environmental variables that have been proposed to influence patterns of resource density and predictability, and for which data are available open access in D-PLACE (Kirby et al. 2016). Climate data for each society reflect annual mean and variance of the Baseline Historical (1900-1949), CCSM ecoClimate model (spatial resolution of 0.5°; Lima-Ribeiro et al. 2015). Net primary productivity (NPP) data reflect annual mean, variance and constancy for each sampled locality from data obtained from the MODIS dataset (spatial resolution of 1km; Running et al. 1999). The distance to coast, elevation and slope data in D-PLACE are derived from the Global Multi-resolution Terrain Elevation Data of the U.S. Geological Survey (U.S. Geological Survey 2010).

We then used principal component analysis to reduce the environmental variables into three composite variables (see Supplementary Table 2). We labeled the three principal components based on the major

contributors to each component. We refer to principal component 1 as “environmental productivity”, as it increases with higher net primary productivity (NPP), higher and more constant temperatures, and more rainfall. We have labeled principal component 2 as “productivity uncertainty” as it increases as the variance in NPP increases and as NPP constancy decreases. The third principal component increases with lower temperatures, and higher elevations and slopes, and we therefore refer to this component as “mountainous”. We also included distance to coast (linear distance to nearest coastline) as a predictor as coastal resources are often dense and predictable (Hassan 1975).

We used population density data from the Binford hunter-gatherer (Binford 2001) and the Standard Cross Cultural Sample (SCCS variable 64; Murdock and Wilson 1972) datasets in D-PLACE (Kirby et al. 2016). The population density data from the Binford dataset are continuous, therefore we coded them based on the categories used in the SCCS data (variable 64). We collected data on political complexity and a variety of environmental variables from D-PLACE. Political complexity reflects the jurisdictional hierarchy variable from the Ethnographic Atlas (variable 33; Murdock 1967, Kirby et al. 2016) and the categories were collapsed to represent 3 levels: 1 = no jurisdictional hierarchy beyond local communities (which is equivalent to the original category 1 = acephalous, none/autonomous bands or villages), 2 = chiefdoms (which is equivalent to the original categories 2 and 3 = petty and larger paramount chiefdoms or their equivalent), 3 = states (which is equivalent to the original categories 4 and 5 = large states).

We included two subsistence variables in the analyses to test for the potential influence of subsistence practices on land ownership norms. For the first subsistence variable we used data on dependence of each society on hunting, gathering, fishing, agriculture and animal husbandry (Ethnographic Atlas variables 1-5 available in D-PLACE; (Murdock 1967, Gray 1999, Korotayev et al. 2004, Bondarenko et al. 2005, Kirby et al. 2016). These variables are available in the form of ordinal scales with each number in the scale referring to a range of percentages representing the portion of a society’s diet that come from the given activity (0 = 0-5%; 1 = 6-15%; 2 = 16-25%; 3 = 26-35%; 4 = 36-45%; 5 = 46-55%; 6 = 56-65%; 7 = 66-75%; 8 = 76-85%; 9 = 86-100%). Because the ranges of percentages add uncertainty to our

understanding of the actual diets, we first generated 100 possible combinations of actual percentage values for each society while ensuring that the total diet (i.e. the sum of the percentages across all subsistence types) added up to 100%. We then used Principal Component Analysis for compositional data (PCA<sub>comp</sub>) (Aitchison and Greenacre 2002) implemented in the R package ‘compositions’ (van den Boogaart and Tolosana-Delgado 2008) to summarize the five subsistence methods into a unique variable. The first dimension from the PCA described an increasing reliance on domesticated resources. We then extracted scores for this first dimension from all the societies used in our analysis and used this as our first subsistence variable. The second subsistence variable describes whether a society practices intensive agriculture, as more intensive agricultural practices have been linked to private land ownership (Boserup 1965). To obtain this variable we used the Ethnographic Atlas variable 028 recorded from D-PLACE (Kirby et al. 2016) and reduced it to a binary variable, where 1 = intensive agriculture and 0 = all other forms.

We also included the settlement pattern of each society as private land ownership may be less likely in more mobile societies (Ember et al. In press). We used variable EA030 from D-PLACE (Murdock 1967, Kirby et al. 2016), and we collapsed the variable to a 5-point ordinal scale: code 1 = nomadic, code 2 = semi-nomadic, code 3 = semi-sedentary, code 4 = impermanent (i.e., villages whose location is shifted every few years), and codes 5-8 = other permanent settlements (including homesteads, hamlets, villages, and complexes). To account for the potential of land ownership practices diffusing across a region via horizontal transmission, we include as a predictor the proportion of the ten nearest neighboring societies that share a society’s land ownership norm (i.e. nearest neighbors’ property system). The model produced analogous results when we varied the number of neighbors used in the calculation (3, 5, 7 and 10 nearest neighbors), and therefore here we only present results using the 10 nearest neighbors to estimate the nearest neighbors’ property system.



In order to assess the relative support for the various hypothesized drivers of land ownership patterns we used multi-model inference procedures (based on logistic regression). We investigated the factors that shape patterns of any type of land ownership (individual, kin-based, or group) against no land ownership norms (Figure 1). Because a robust phylogeny does not exist for all the world's languages, we included language family as a random effect in the models to control for the non-independence of societies that share a common cultural background.

After running all possible model combinations for each dataset, the AIC weight (AICw) of the best supported model was less than 0.9 in all cases, suggesting model averaging is an appropriate approach (Burnham and Anderson 2010). Some of the variables included in our dataset may be collinear (e.g. dependence on agriculture and population density) and this has the potential to complicate analyses. However, the model averaging approach is not sensitive to low or moderate levels of collinearity when effects of variables are similar (Freckleton 2011). Tests for collinearity confirm that model averaging is appropriate (variance inflation factors range between 2-3). The models with  $\Delta AICc$  less than 10 were selected for model averaging (Bolker et al. 2009, Burnham and Anderson 2010). We found no evidence of spatial autocorrelation in model residuals (see Supplementary Figure 1).

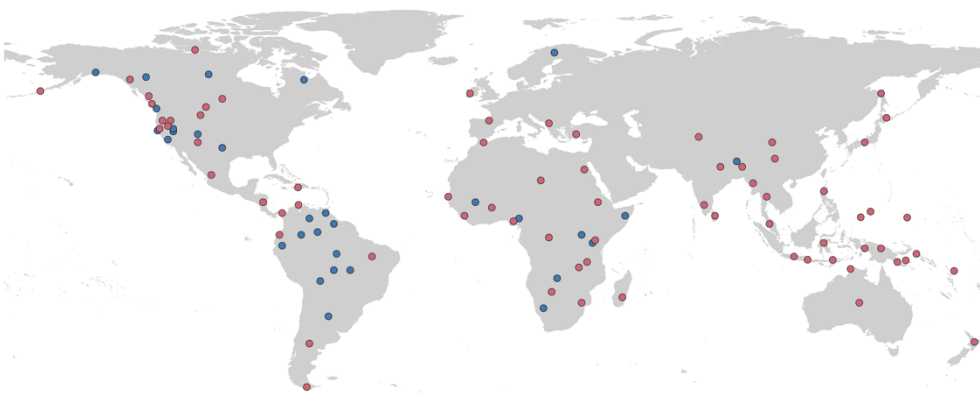
## Results

We found three variables – nearest neighbors' property system, population density, and mountainous - had a significant association with land ownership practices in our averaged model (Table 1, Supplementary Table 1, and Figure 2). Population density and the nearest neighbors' property system also had a relative variable importance of 1, indicating that these variables occurred in all models that we averaged across. Population density had a significant relationship with the presence of some form of land ownership, suggesting that competition for land may influence the likelihood of all forms of land ownership. Our model predicts that societies with population densities  $<0.07$  people/km<sup>2</sup> will have greater

than a 75% probability of no land ownership. However, societies that maintain population densities  $>193.05$  people/km<sup>2</sup> will have nearly a 100% probability of some form of land ownership (Figure 2a).

The probability of land ownership was also significantly associated with the nearest neighbors' property system. When greater than 50% of nearest neighbors had a given form of land ownership, a society had a greater than 50% probability of sharing that same form of ownership (Figure 2c). The probability of having some form of land ownership also increases in more mountainous environments (see Table 1, Figure 2b), and the relative variable importance is 0.88 with the variable appearing in 127 of the 204 models we averaged.

None of the other variables we tested (environmental productivity, environmental uncertainty, distance to coast, political complexity, reliance on domestication, intensive agriculture, and settlement pattern) were significant in our averaged model and all had a relative variable importance  $<0.75$ . Overall, the suite of variables included described the majority of the variation in land ownership norms among the societies tested ( $R^2 = 0.69$ ). We found no difference in the fit statistics between our full model and a model that excluded the random effect of language family (i.e.,  $R^2$  conditional and  $R^2$  marginal both equal 0.69).

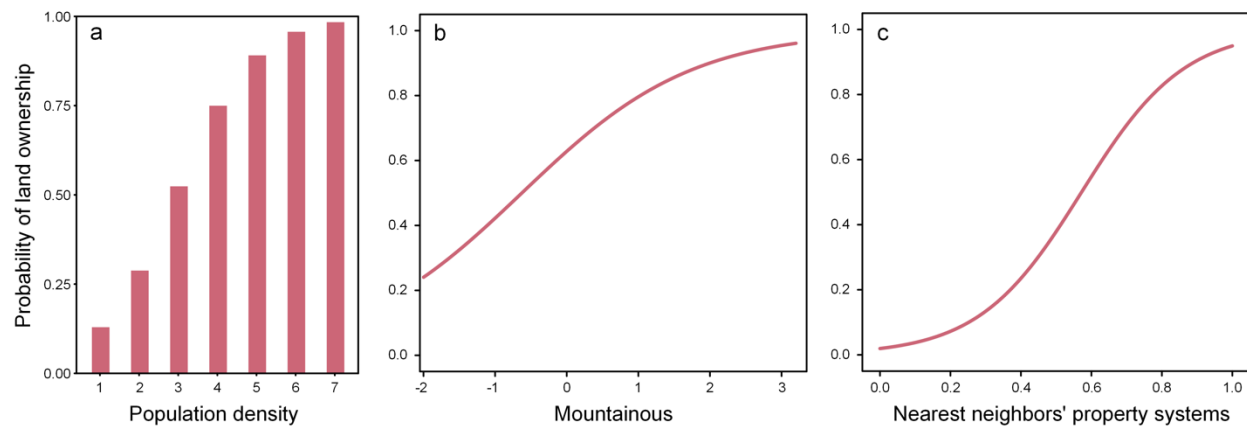


**Figure 1.** Geographical distribution of societies with land ownership (red, n=71) and with no land ownership (blue, n=31).

**Table 1.** Multi-model average results for analysis of any form of land ownership versus no land ownership norms.  $n = 102$ . Standardized coefficients are presented. Marginal  $R^2$  represents variation captured by fixed effects alone, conditional  $R^2$  represents variation captured by both fixed and random effects.

Parameter	$\beta$ coefficient	Standard error	$p$ -value	RVI
Intercept	-5.11	1.69	<0.01	1.00
Nearest neighbors' property system	6.86	2.01	<0.001	1.00
Population density	1.00	0.35	<0.01	1.00
Mountainous	0.84	0.37	<0.05	0.88
Environmental productivity	-0.83	0.42	>0.05	0.74
Distance to coast	-0.64	0.33	>0.05	0.71
Environmental productivity uncertainty	-0.44	0.34	>0.1	0.43
Settlement pattern	-0.28	0.27	>0.1	0.36
Political complexity	-0.72	0.76	>0.1	0.33
Reliance on domestication	-0.39	0.60	>0.5	0.29
Intensive agriculture	-0.49	1.19	>0.5	0.26

$R^2_{\text{glmm}}$ : marginal = 0.69; conditional = 0.69



**Figure 2.** Predicted probabilities of land ownership with increasing population density (a), more mountainous environments (b), nearest neighbors' property system (i.e., proportion of neighbors with the same land ownership norms) (c). Population density categories are as follows: 1) <0.07 people/km<sup>2</sup>; 2) 0.39-0.08 people/km<sup>2</sup>; 3) 0.39-1.93 people/km<sup>2</sup>; 4) 1.94-9.65 people/km<sup>2</sup>; 5) 9.6-38.61 people/km<sup>2</sup>; 6) 38.62 -193.05 people/km<sup>2</sup>; 7) >193.05 people/km<sup>2</sup>.

## Discussion

We found an increased probability of land ownership in mountainous environments, and when societies live at higher population densities (see Figure 2). The increased probability in mountainous regions might

appear to contradict resource defensibility theory (Rose 1998, Acheson et al. 2015), as we might expect mountains to have resources in lower densities and to possess less arable land. However, specific resources in mountains often have patchy distributions, as availability can change rapidly over short distances when slopes increase. In addition, useable resources for a given human group may be limited to a restricted elevational range due to niche partitioning, in which human groups focus on exploiting specific resources in a given elevation range. Also, as slopes increase, arable land and human movement may be more limited, which would create an incentive to secure tightly packed resources via land ownership. Patchy resources, such as those in many mountainous regions, are often aggregated, and competition can be fierce for the most valuable patches (Cashdan et al. 1983). In turn, the benefits of defending resources in these environments may outweigh the costs; and therefore, as predicted by resource defensibility theory, these regions may be more prone to land ownership, as we find.

We suggest that future studies develop a broader range of metrics for capturing the concept of resource defensibility and explore the degree to which the metrics chosen influence the conclusions reached. Although the measures of environmental productivity and predictability that have been used in prior studies (e.g., Ember et al. In press, Cashdan et al. 1983, Freeman and Anderies 2015) can theoretically influence potential defensibility and the ability to gather adequate information on resources, the degree to which resources are spatially clustered and the techniques used to assess and gather resources will also shape defensibility.

Higher population densities may also increase pressure on natural resources. The population densities of societies in our dataset varied widely ( $<0.07$  people/km<sup>2</sup> to  $>193.05$  people/km<sup>2</sup>), and those living at higher densities also had a greater probability of owning land (Figure 2a). This land ownership may provide a mechanism to alleviate the stress caused by the resource competition arising from higher population densities (Boserup 1965, Hardin 1968, Guillet 1981, Rosenberg 1990).

However, contrary to resource defensibility theory, we did not find any significant relationships for other measures of resource availability, including environmental productivity, distance to coast and environmental uncertainty. Although we did not uncover any substantial issues with multicollinearity between population density and these other variables, perhaps the population density variable we used accounted for the cumulative effects of multiple factors shaping resource availability (e.g., environmental productivity, seasonality, distance to coast), as well as differences in lifeways among societies (e.g. mobility, subsistence). Prior research has found that all these variables may be linked in complex causal pathways that together shape population density (Kavanagh et al. 2018).

Recent research into the evolution of land tenure norms among Austronesian societies suggests that vertical transmission (i.e. inheritance) has played a role in shaping patterns of kin-based land tenure (Kushnick et al. 2014). Similarly, a global study of hunter-gatherer societies (Freeman and Anderies 2015) noted that groups that share common ancestry, tend to share similar land ownership norms. We found that the conditional fit of our model, which accounts for the random effect of language family, was the same as the marginal fit that did not include the random effect. However, because closely related societies tend to live closer together, and thus in similar environments, the variance explained by phylogeny, environment, and neighbors' property systems also tends to be shared. Therefore, while we can conclude that phylogeny, environment (e.g., mountainous regions), and nearest neighbors' property systems may all be associated with land ownership, it is statistically difficult to say which of these three factors has more influence than the others.

We also find that, on a global scale, land ownership practices are associated with the land ownership norms of nearby societies. This finding is in contrast to the situation among Austronesian societies, where the geographic distances between societies did not influence land tenure practices (Kushnick et al. 2014).

Through direct observation and horizontal transmission of knowledge, cultural traits can be rapidly spread among human groups that have regular contact. This allows societies to adopt practices that have clear advantages within a given context. However, we also cannot dismiss the possibility that the significance of the nearest neighbors' property system variable is in part due to other context-specific variables that societies in the same region hold in common, including aspects of the environment we did not have data on for our focal societies (e.g., soil fertility, biodiversity, water resources). Another alternative mechanism could involve increased pressure on resources leading to neighbors attempting to take resources through warfare, which may pressure neighboring groups to exert property rights in similar ways (Ember et al. 1974, Freeman and Anderies 2015).

Our sample size and the number of variables for which we could obtain sufficient data do place some important limitations on our analyses. For one, we were not able to explore differences among societies that hold different forms of land tenure (e.g., private vs. communal vs kin-based) as has been examined in recent research (Ember et al. In press). Ember et al used a different dataset, which had minimal overlap with the societies in our study, to analyze factors associated with individual versus communal land rights, including rights to use land, to alter land, to exclude others from land, and to transfer land. Ember et al. also highlight the importance additional variables may play in influencing individual versus communal tenure, but we did not have sufficient data to include these variables in our analyses of no versus some land ownership. These additional variables include alternative measures of intensification, including arboriculture, fish weirs, and terracing. Natural hazards (e.g., drought) can also contribute to defensibility of resources, as more hazards can reduce the reliability of a society's resource base over time (Ember et al. In press). In addition, residence rules (i.e. where married couples live: with family of parents or not) and norms of descent (e.g., lineal vs non-lineal models) may determine how many near kin live together or nearby, and thus may influence kin-based defense of land (Ember et al. In press, 1974). Future research with larger datasets might be able to include this suite of variables, as well as explore more complex

causal pathways in which, for example, environmental variables influence land ownership directly and indirectly via their effects on mobility, population density, and subsistence strategies.

Here we used theory developed in part in ecology and methods commonly used in biogeography to explore possible factors associated with land ownership in human groups. The recent publication of large open-access databases (e.g., [www.d-place.org](http://www.d-place.org); Kirby et al. 2016)) that link maps of thousands of human societies and data on thousands of their cultural traits with environmental variables from the same locations open up the potential for biogeographers and macroecologists to explore an incredible array of different facets of human cultural diversity and to contribute to long-standing debates among many different academic fields about the mechanisms shaping human diversity.

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**Supplementary Table 1.** The 102 societies included in the analyses of land ownership patterns. All data obtained from D-PLACE ([www.d-place.org](http://www.d-place.org)).

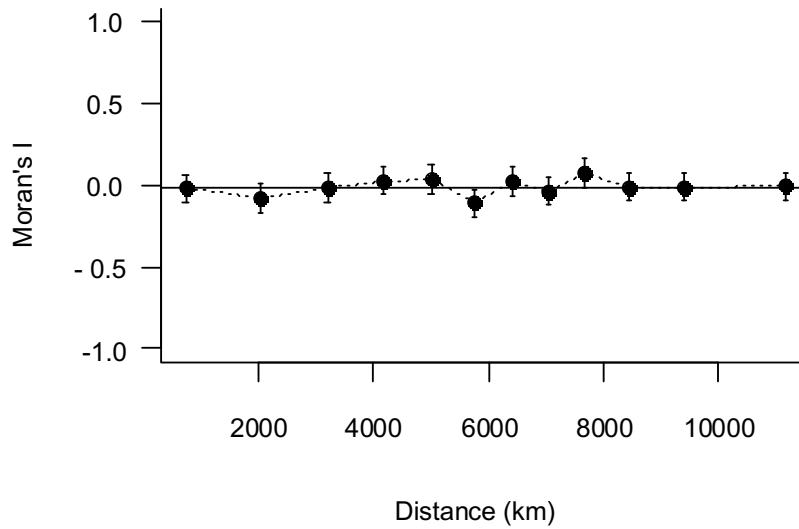
Society name	Latitude	Longitude	Language family	Main land ownership norm
!Kung	-20	21	Southern Africa	Group
Abipón	-29	-61	Guaicuruan	None
Ainu	44	144	Language isolate	Group
Aleut	53.86	-166.79	Eskimo-Aleut	Kin
Alorese	-8.22	124.26	Austronesian	Individual
Amhara	13	38	Afro-Asiatic	Individual
Assiniboin	48	-106	Siouan	Group
Balinese	-8.18	115.02	Austronesian	Individual
Bambara	13	-7	Mande	None
Barama River Carib	5	-59	Cariban	None
Bemba	-11	31	Atlantic-Congo	Individual
Bungi	51	-100	Algic	Group
Burmese	20	95	Sino-Tibetan	Kin
Burusho	37	75	Language isolate	Individual
Canela	-7	-45	Jean	Individual
Chachi	1	-79	Barbacoan	Individual
Chugach	60.72	-146.49	Eskimo-Aleut	None
Coast Yuki	39.34	-123.77	Yukian	None
Comanche	33	-100	Uto-Aztecan	None
Copper Inuit	69	-110	Eskimo-Aleut	Group
Crow	45	-108	Siouan-Catawban	Individual
Cubeo	1	-71	Tucanoan	None
Dene	60	-105	Eyak-Athabaskan	None
Egyptians	25	33	Afro-Asiatic	Individual
Ganda	1	32	Atlantic-Congo	None
Garo	26	91	Sino-Tibetan	Kin
Gheg	42	20	Indo-European	Individual
Guna	9	-78	Chibchan	Individual
Haitians	18.41	-72.17	Creole	Individual
Huichol	23	-104	Uto-Aztecan	Group
Ifugao	17	121	Austronesian	Kin
Igbo	6	7	Atlantic-Congo	Kin
Irish	53	-9	Indo-European	Individual
Japanese	35	136	Japanic	Kin
Javanese	-7	110	Austronesian	Kin
Kaska	59	-128	Eyak-Athabaskan	None
Kikuyu	-1	37	Atlantic-Congo	Individual
Klamath	43	-122	Language isolate	Group

Koreans	35	102	Language isolate	Individual
Kwoma	-4	142	Sepik	Kin
Lepcha	28	89	Sino-Tibetan	None
Lolo	29	103	Sino-Tibetan	Kin
Lozi	-15	23	Niger-Congo, Atlantic-Congo	None
Maasi	-2	36	Nilo-Saharan, Eastern Sudanic	None
Māori	-38.41	176.31	Austronesian	Kin
Mapuche	-39	-68	Mapudungu	Kin
Mee	-4	136	Trans-New Guinea	Individual
Mende	8	-11	Mande	Kin
Miskito	13	-85	Misumalpan	Individual
Munduruku	-6	-58	Tupian	None
Nama	-26	18	Southern Africa	None
Nambikwara	-12	-59	Nambiquaran	None
Naskapi	58	-70	Algic	None
Nivkh	53	142	Language isolate	Kin
Nkundo	0	20	Niger-Congo, Atlantic-Congo	Individual
Nootka	49.16	-125.85	Wakashan	Kin
Northern Aranda	-24	134	Pama-Nyungan	Group
Nuxalk	52	-127	Salish	Kin
Nyakyusa	-9	34	Atlantic-Congo	Group
Orokaiva	-9	148	Trans-New Guinea	Kin
Palauans	7.45	134.54	Austronesian	Kin
Pumé	7	-68	Unclassified	None
Quinault	47.42	-124.16	Salish	None
Riffians	35	-4	Afro-Asiatic	Individual
Sami	68	22	Uralic	None
Semang	5	101	Austro-Asiatic	Kin
Shuar	-3	-78	Jivaroan	None
Sirionó	-16	-64	Tupian	None
Siuai	-6	155	South Bougainville	Kin
Somali	8	48	Afro-Asiatic	None
Southern Ute	38	-109	Uto-Aztecan	None
Spanish Basques	43	-2	Language isolate	Individual
Tallensi	11	-1	Atlantic-Congo	Kin
Tanala	-22	47	Austronesian	Kin
Teda	21	17	Nilo-Saharan, Saharan	Kin
Thai	15	100	Tai-Kadai	Individual
Tikopia	-12.29	168.83	Austronesian	Kin
Tiv	7	9	Atlantic-Congo	None
Tiwi	-11.56	130.81	Tiwian	Kin

Tlingit	58.12	-133.92	Language isolate	Kin
Toda	12	77	Dravidian	Kin
Toedokado	40	-118	Uto-Aztecan	None
Toradja	-2	121	Austronesian	Group
Trobriands	-8.43	151.09	Austronesian	Kin
Trukese	7.34	151.6	Austronesian	Kin
Trumai	-12	-53	Language isolate	None
Tsonga	-24	32	Atlantic-Congo	Individual
Tübalulabal	39	-118	Uto-Aztecan	None
Turks	38	30	Altaic	Kin
Uttar Pradesh	26	83	Indo-European	Individual
Vedda	8	81	Indo-European	Group
Wadadokado	43	-119	Uto-Aztecan	Group
Wadatkuht	41	-120	Uto-Aztecan	Group
Warao	9	-62	Language isolate	None
Wayuu	12	-72	Maipurean	Kin
Wolof	15	-17	Niger-Congo, Atlantic-Congo	Kin
Yahgan	-55.02	-68.98	Language isolate	Group
Yanomamo	2	-65	Yanomaman	None
Yapese	9.55	138.13	Austronesian	Individual
Yokuts	36	-120	Yokutsan	None
Yuki	40	-123	Yukian	Group
Zuni	35	-109	Language isolate	Individual

**Supplementary Table 2.** Results of Principal Components Analysis of environmental variables with varimax rotation.

Variable	Environmental productivity (PC1)	Productivity uncertainty (PC3)	Mountainous (PC2)	Uniqueness
sqrt (k - annual mean temperature)	<b>-0.70</b>	0.16	<b>0.58</b>	0.147
ln (annual temperature variance)	<b>-0.85</b>	-0.02	0.37	0.141
sqrt (annual mean precipitation)	<b>0.86</b>	0.28	0.06	0.176
ln (annual precipitation variance)	<b>0.85</b>	0.24	0.10	0.219
sqrt (annual mean npp)	<b>0.68</b>	<b>0.57</b>	-0.14	0.190
sqrt (annual mean npp variance)	0.01	<b>0.98</b>	0.03	0.038
sqrt (npp constancy)	-0.45	<b>-0.84</b>	0.12	0.073
sqrt (elevation)	-0.14	-0.19	<b>0.85</b>	0.225
sqrt (slope)	0.04	0.05	<b>0.90</b>	0.189
SS loadings	3.35	2.19	2.06	
Cumulative variance	0.37	0.62	0.84	



**Supplementary Figure 1.** Moran's I by distance for model residuals from global model (i.e. full model prior to model averaging).