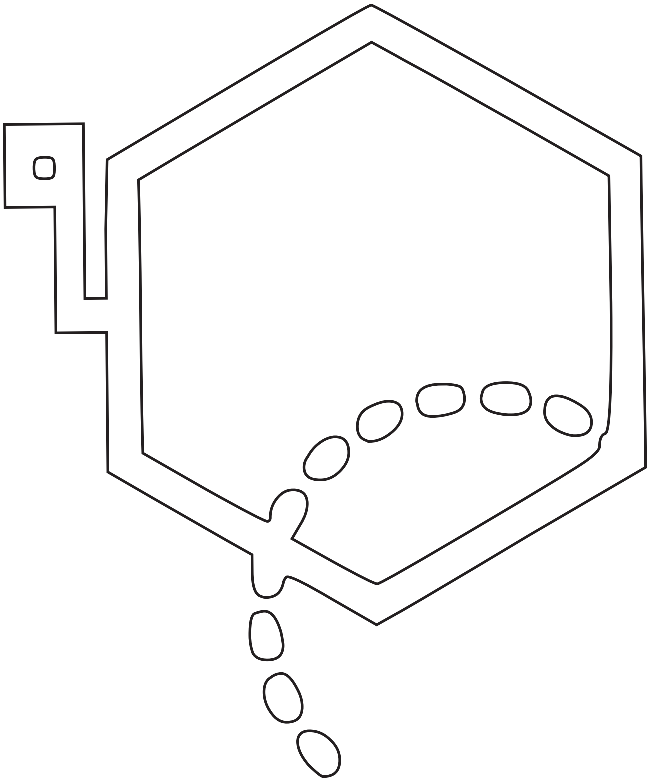

5

ECOLOGICAL AND SOCIAL DYNAMICS OF TERRITORIALITY AND HIERARCHY FORMATION

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The origins of complex societies—those with hierarchically organized political systems, specialized divisions of labor, and relatively unequal distributions of power and wealth—fascinate us. These societies tend to be politically and socially integrated at very large scales, encompassing tens of thousands to hundreds of millions of individuals. They are the societies in which most of us live.

It hasn't always been this way. For 92 to 98 percent of the existence of modern *Homo sapiens*, it appears that most people lived in relatively small-scale, egalitarian societies, with muted differences in wealth, status, and political power (Boehm 2001; Smith et al. 2010). What happened? Why did it happen? These are longstanding questions, ones that this chapter attempts to address in a systematic and novel way.

Every state that exists today is a cultural successor to the earliest states that arose during the Middle Holocene. Each of these states grew on an economic foundation of intensive agriculture cultivated on well-watered, fertile land (Trigger 2003). Agriculturalists, however, are not the only societies to manifest political complexity and inequality.

Despite the fact that most foragers (i.e., hunter-gatherers) known in recent history live in relatively small-scale, egalitarian groups, foragers are also capable of generating hierarchical and unequal societies. Among foragers of the Pacific coast of North

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America, multivillage political units encompassing 100 to 10,000 individuals were led by chiefs and exhibited a complex continuum of social rank, slavery, and a significant degree of economic inequality. These foragers relied on resource-producing sites—salmon runs, fruit and nut groves, and coastal sites for maritime hunting and foraging—that were predictably clustered in space and time. This spatial and temporal concentration of resources motivated territorial claims and hierarchically organized, large-scale warfare over access to prime sites (Gunther 1972; Ames 1994; Matson and Coupland 1994: Rick et al. 2005; Kennett 2005).

The common denominator of political complexity among agriculturalists and foragers—the value of claiming and defending durable, defensible resources and resource-producing sites—underlies the central thesis of this chapter: *the social dynamics that arise in the context of economically defensible resources are key generators of large-scale political integration and political hierarchy.*

We establish the theoretical validity of this thesis with a computational model based on a set of simple assumptions. The model identifies features of the natural, social, and technological environment that favor (or disfavor) the development of an arms race between larger and more hierarchically organized territorial coalitions. The following three sections describe the model, summarize its results, then discuss the implications for understanding hierarchy and state formation in human history.

The Model

OVERVIEW

This model represents the cultural evolution of different strategies for gaining access to resource sites. These strategies vary in whether or not they attempt to (1) territorially defend sites, (2) form territorial alliances, and (3) establish territorial political hierarchies (Figure 1 and Table 1). The exogenous parameters of the

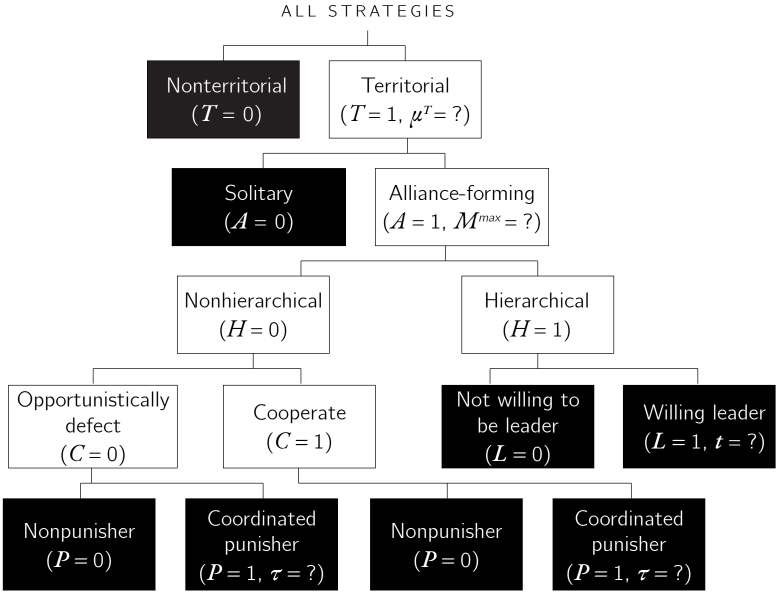


FIGURE 1 A nested taxonomy of strategy types. The black (terminal) nodes indicate fully specified strategy types. The subscript i can be added to any of these variables to indicate the value of individual i. The question marks (?) indicate continuous values that vary across individuals.

TABLE 1 Evolving strategies and decision variables for individual i.

Strategy	Symbol	Values	Associated decision variable	Symbol	Values
Territorial	T_i	0, 1	Contest threshold	μ_i^T	0–1
Alliance-forming	A_i	0, 1	Maximum alliance size	$M_i^{\max}$	0–N
Cooperate	C_i	0, 1	–	–	–
Coordinated punisher	P_i	0, 1	CP coordination threshold	τ_i	0–N
Hierarchical	H_i	0, 1	–	–	–
Willing leader	L_i	0, 1	Tax offered as leader	t_i	0–∞

TABLE 2. Exogenous socioecological parameters.

	Parameter	Symbol	Values
Focal	Variance in patch productivity	var(μ_k)	0.005, 0.030, 0.055
	Decisiveness of alliances	α	1, 2, 4
	Base cost of alliance*	c^A	0.05, 0.15, 0.25
	Cost of cooperation*	c^C	0.05, 0.35, 0.65
	Cost of enforcement*	c^E	0.05, 0.35, 0.65
	Efficiency of leadership selection process	d	0, 0.5, 1
Additional	Landscape dimensions (in patches)	$x \times x$	33 × 33
	Mean patch productivity	mean(μ_k)	0.1
	Clustering of productive patches	S	0.1, 0.2, 1.0
	Spatial reach†	r	0.12, 0.36, 0.6
	Intrinsic rate of increase coefficient	B	4
	Rounds per generation	–	25
	Generations per run	–	250
	Probability of mutation	–	0.01

*In units of μ; †In units of x.

TABLE 3. Other variables in the model.

Variable	Symbol	Values
Total number of agents	N	0–∞
Number of agents on patch k	N_k	0–N
Number of allies of i	M_i	0–N
Number of active defectors in i's alliance	M_i^D	0–N
Number of willing punishers in i's alliance	M_i^P	0–N
There are ≥ 1 willing punishers in i's alliance	$\hat{P}(1)$	0, 1
There are ≥ τ_i willing punishers in i's alliance	$\hat{P}(\tau_i)$	0, 1
Number of followers of i	F_i	0–N

model are intended to reflect variation in the social and ecological circumstances faced by human groups according to time and place (Table 2). The economic defensibility of sites is represented in terms of the variance in the expected productivity of resource patches. Whether or not agents form alliances to claim and defend territory depends on this variance in the quality of land (or "patchiness"), as well as the costs of maintaining and cooperating within alliances. Whether or not individuals are willing to buy into systems of political hierarchy that monitor and enforce the cooperation of alliance members depends on the relative efficiency and costs of hierarchy compared to nonhierarchical alternatives.

The current model synthesizes the theories of economic defensibility and animal contests (Brown 1964; Maynard Smith and Price 1973; Dyson-Hudson and Smith 1978; Boone 1992) with models of the evolution of cooperation, punishment, and political hierarchy from evolutionary anthropology (Smith and Choi 2007; Hooper et al. 2010; Boyd et al. 2010). The model nests the strategies and replicator dynamics of evolutionary game theory (McElreath and Boyd 2007; Gintis 2009) within a simulation in NetLogo 5.1.0 with explicit spatial and demographic dynamics (Wilensky 1999). This model builds on the base of previous evolutionary models by representing explicit landscapes with productivity that varies in space and time; endogenous returns to scale in competition for territorial resources; and a statistical analysis of stochastic outcomes as a function of socioecological parameters. Like all useful models, it aims to establish clear principles that sharpen our understanding of real-world phenomena, rather than recreate the full complexity of reality itself.

SOCIOECOLOGY

The socioecology of the model is defined by the spatial variability of resource production and an array of parameters affecting the benefits and costs of different social behaviors (Table 2). The exogenous nature of these parameters allows a principled statistical analysis of the results and avoids issues of inference under endogeneity.

The spatial landscape of the model is defined as an $x \times x$ torus containing x^2 patches. In each round, each patch k produces one resource unit (productivity $L_k = 1$) with probability μ_k and produces nothing ($L_k = 0$) with probability $1 - \mu_k$. The spatial distribution of mean productivity μ_k (equal to the probability of producing a resource in each round) is taken as an exogenous characteristic of ecology. The present analysis employs a set of nine landscapes, specified in terms of the spatial distribution of μ_k (Figure 2). These landscapes have the same overall mean productivity of patches mean(μ_k) but different values for both the "patchiness" of the landscape (i.e., variance in productivity across patches: var(μ_k)) and the extent to which productive patches cluster together in space (S). To generate these landscapes, the product of two orthogonal sine waves (both with the same frequency tuned by the parameter S) was raised to a power Φ ($0 < \Phi < 20$), then renormalized to achieve the target values of mean(μ_k) and var(μ_k). While the theory of economic defensibility emphasizes variance in resource production across both space and time, for simplicity, the current model focuses only on spatial variance; its main results, however, can easily be reinterpreted in terms of temporal variability (or predictability), with some important differences discussed in Dyson-Hudson and Smith (1978).

STRATEGIES AND INTERACTION

The landscape is seeded with a small number of nonterritorial agents, interpretable as single individuals or family units. In each nonoverlapping generation, agents interact over multiple rounds (default = 25). In each round, in random order, each agent attempts to move to an undefended patch, claim a defended patch, or stay in place, depending on its inherited strategy types and decision variables (Figure 1 and Table 1).

Each agent i employs either a nonterritorial strategy ($T_i = 0$) or a territorial strategy ($T_i = 1$). Nonterritorial agents attempt to move to (or stay on) an undefended patch within their spatial reach (r) that yields the highest per capita productivity (L_k/N_k, where N_k is the number of agents occupying patch k). Nonterritorial agents are thus facultatively nomadic, moving when productivity can be improved and staying when local productivity remains high.

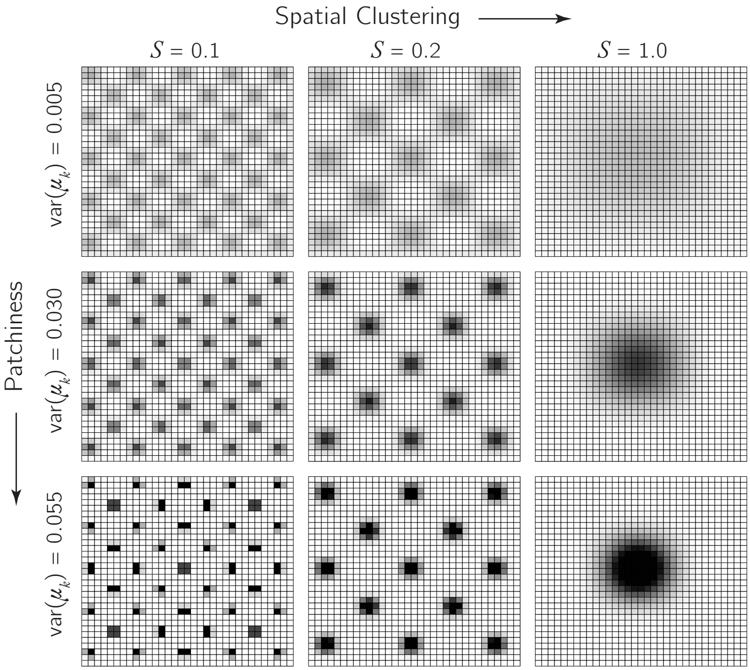


FIGURE 2 Nine ecologies differing in patchiness, var(μ_k), and spatial clustering of productive patches, S. Patchiness increases from top to bottom, while clustering increases from left to right. The mean productivity of each landscape, mean(μ_k), is held constant at 0.1.

Territorial agents that have not claimed a patch first attempt to find an undefended patch within their spatial reach that has expected productivity greater than or equal to their heritable contest threshold (i.e., $\mu_k \geq \mu_i^T$). If an acceptable undefended patch is available, they occupy and claim the patch. If no acceptable patch is found, they attempt to find an already-defended patch within their spatial reach for which $\mu_k \geq \mu_i^T$. If an acceptable patch is found, they contest the existing claimant for ownership. The strength of an agent in contesting a patch depends on whether it employs a solitary strategy ($A_i = 0$) or an alliance-forming strategy ($A_i = 1$). The strength of solitary agents contesting patches is equal to 1. The strength of alliance-forming agents is equal to 1 plus the number of alliance partners that cooperate in contesting the patch.

Prior to a contest, an alliance-forming agent i that has fewer than $M_i^{\max}$ alliance partners attempts to recruit additional alliance partners. Nonhierarchical agents ($H_i = 0$) form alliances with other nonhierarchical agents, while hierarchical agents ($H_i = 1$) form alliances with hierarchical agents. Alliance partnerships (i.e., edges in an alliance network or graph) require pairwise stability as defined in Jackson (2008). Thus, if there is an alliance-forming agent j within i's spatial reach who is not already claiming a patch, has fewer than $M_i^{\max}$ alliance partners , and is able to find a patch adjacent to the patch targeted by i that is above its contest threshold μ_j^T, then i and j become linked in an offensive alliance. This process repeats until i attains $M_i^{\max}$ alliance partners , or no further partners can be found. Once i and their M_i alliance partners have targeted a set of defended patches, each defender p that forms alliances and has fewer than $M_p^{\max}$ partners attempts to recruit additional partners. New defensive alliance partners are required to occupy patches adjacent to p or another member of p's alliance.

Once alliances have formed, a series of $(1 + M_i)$ contests are played out between the offensive and defensive alliances, one for each patch targeted by the members of i's alliance. The strength of i's alliance σ_i is the sum of i's own effort and the effort of those alliance members who are cooperative either by heritable strategy (i.e., $C_i = 1$) or because their cooperation is enforced by coordinated punishers or a hierarchical leader. If M_i^D is the number of active defectors (opportunistic defectors whose cooperation is not enforced), then the strength of the alliance is $\sigma_i = 1 + M_i - M_i^D$.

Cooperation within nonhierarchical alliances can be enforced by the action of coordinated punishers (for whom $P_i = 1$). As in Boyd et al. (2010), a coordinated punisher is willing to expend the effort to enforce cooperation when there are least τ coordinated punishers present in the alliance, where τ is a heritable decision variable held by the coordinated punisher. The cost of enforcing the cooperation of each of M^D opportunistic defectors, $c^E M^D$, is divided evenly among the willing coordinated punishers in the alliance (i.e., $c^E M^D / M^P$ per punisher).

Cooperation within hierarchical alliances can be enforced through the action of a leader. A leader is selected among those members of the hierarchical alliance who are willing to lead (for whom $L_i = 1$). Each potential leader offers a heritable per capita tax (t_j, defined as a fixed amount rather than a fraction or rate), which is observable to alliance members.

Which potential leader is selected depends on the parameter d reflecting the efficiency of the process that selects leaders within groups. When this process is maximally efficient ($d = 1$), the leader who offers the lowest tax is selected; when $d = 0$, the leader who offers the highest tax is selected; intermediate values of d select the leader closest to that quantile value (e.g., $d = 0.5$ selects the leader offering the median tax). The parameter d can be interpreted as the extent to which alliance members are able to select the most efficient or generous leaders through a low-cost, democratic process (or alternatively as the accuracy of individual's perceptions of the true tax rates). The leader receives a tax t_j paid by each of the F_i other group members (followers) and pays a cost $c^E M^D$ to enforce the cooperation of M^D opportunistic defectors in the alliance. If no members of a hierarchical alliance are willing to lead, the alliance operates as a nonhierarchical alliance, in which cooperation either remains unenforced or is enforced through coordinated punishment.

The probability that i is successful in a contest against p is decided by the contest-success function $\sigma_i^\alpha/(\sigma_i^\alpha + \sigma_p^\alpha)$ (Hirshleifer 2001). The exponent α in this expression represents the decisiveness of alliances in determining the outcome of contests. When α is greater, the slope of the content success function around the inflection point (where the two alliances are of equal strength) is steeper, reflecting more of a winner-take-all environment. α thus reflects the importance of the relative size of the alliance for determining the outcome of the conflict. If the offensive agent is successful, it takes exclusive claim of and occupies the patch, while the defensive agent is ejected to a randomly chosen undefended patch. If the defensive agent is successful, neither move. Members of an offensive alliance that successfully claim new patches remain linked as allies once they have settled on their new territories. Members of defensive alliances that are not ejected from the patches they claim also remain linked as allies following the contest.

At the end of each round, the resources produced by each patch are divided equally among its occupants and added to their cumulative lifetime fitness. Successful territorial agents enjoy the benefit of not having to share with others but must pay the costs of having to claim and defend the land. The per-round contribution to fitness of individual i occupying patch k (equation 1) is thus equal to the per capita productivity of patch k (first term: L_k/N_k) minus the costs of their strategy- and context-dependent behavior: the costs of maintaining alliances (second term: $c^A M_i$);

the cost of cooperating to defend territory, whether dictated by strategy or stimulated by enforcement (third term: $c^C\max(C_i, H_i, \hat{P}(1))$); the coordinated punisher's cost of enforcing the cooperation of each opportunistic defector (fourth term: $c^E\hat{P}(\tau_i)M_i^D/M_i^P$); and the hierarchical agent's cost of being taxed (fifth term: t_jH^i). Hierarchical agents who enforce cooperation as leaders also receive the benefit of taxation minus the cost of enforcement for each of F_i followers (sixth term: $(t_i - c^EM_i^D/M_i)F_i$). The individual's per-round contribution to fitness w_i is defined by equation (1):

$$\begin{aligned} w_i = L_kN_k - c^AM_i - c^C\max\left(C_i, H_i, \hat{P}(1)\right) \quad (1) \\ - \hat{P}(\tau_i)c^EM_i^D/M_i^P - t_jH_t + (t_i - c^EM_i^D/M_i)F_i \end{aligned}$$

REPRODUCTION

After a generation has interacted through multiple rounds, each agent's fitness W_i is calculated as the mean of their contributions to fitness across rounds multiplied by B, a coefficient affecting the intrinsic rate of increase: $W_i = B \times \text{mean}(w_i)$. Each agent produces a whole number of offspring equal to the integer part of W_i, and produces an additional offspring with probability equal to the fractional part of W_i. Offspring are distributed randomly on the landscape.

Offspring inherit their parent's strategies and decision variables, with an independent probability of mutation (default = 0.01) for each variable. Mutations of strategy variables switch between 0 and 1; mutations of the contest threshold μ_i^T and tax offered as leader t_i increase or decrease by 0.01 with equal probability; and mutations of the maximum alliance size $M_i^{\max}$ and the coordinated punisher's coordination threshold τ_i increase or decrease by 1. The older generation dies, territorial claims and alliances are reset, and the new generation begins in round 1.

SAMPLING AND ANALYSIS

The analyses of the simulation in the following section characterize the effects of different socioecological parameters on the principal outcomes of the model, as they evolve through time (Figure 3) and after a long period of evolution (Figures 4 and 5; see also Appendix, p. 306).

To produce the historical trajectories plotted in Figure 3, runs of 250 generations playing 25 rounds per germination were simulated in each of four contrasting socioecologies. Ecology (A) has low patchiness, as well as as low costs of alliance formation, cooperation, and hierarchy. Ecologies (B), (C), and (D) have very patchy landscapes, but vary in terms of the costs of social interaction. Ecology (B) has high costs of cooperation and enforcement and inefficient political institutions; ecology (C) has low costs of cooperation, but high costs of enforcement and inefficient political institutions; while ecology (D) has low costs of cooperation and enforcement and efficient political institutions.

For the statistical analysis of long-run outcomes summarized in Figures 4 and 5, 200 runs of 250 generations playing 25 rounds per generation were parameterized by randomly sampling the parameter values given in Table 2 (see also Appendix, p. 306). For each parameter (with the exception of landscape patchiness) one of three values was sampled with equal probability. For the landscape patchiness, var(μ_k), the high-variance condition was sampled at twice the rate of the medium- and low-variance conditions, to better explore subtleties in the conditions underlying the formation of competitive alliances and hierarchies. Long-run strategy frequencies, mean alliance sizes, and inequality were estimated as a function of socioecological parameters using regression. Inequality was measured as the Gini coefficient of fitness, Gini(W), using the redist package (Handcock 2015). For the analyses of strategy frequencies and alliance sizes in table in the Appendix, p. 309, the lmer function in the lme4 package (Bates et al. 2013) was used to estimate outcomes in the last 100 generations of each run, including a random effect to capture the nonindependence of outcomes across generations within each run

Results

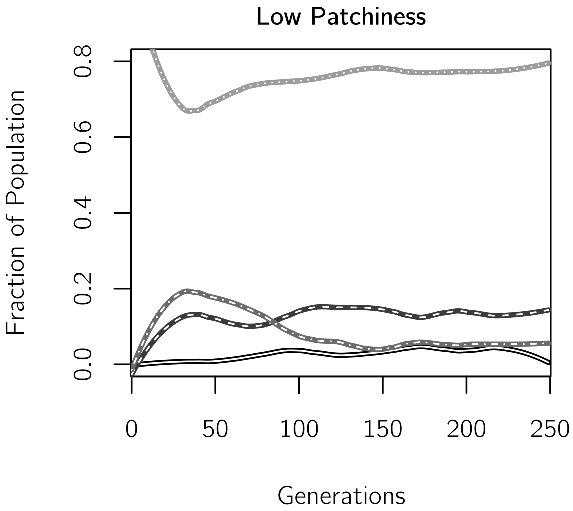
HISTORICAL DYNAMICS

The effects of ecological and social parameters on the population dynamics of nonterritorial and territorial agents are illustrated across panels A, B, C, and D in Figure 3. Environment A is characterized by a relatively homogeneous distribution of productivity across the landscape (the landscape in the first row, middle column of Figure 2). In this environment, nonterritorial agents retain the advantage over territorial strategies, maintaining a long-run mean of around two-thirds of the population.

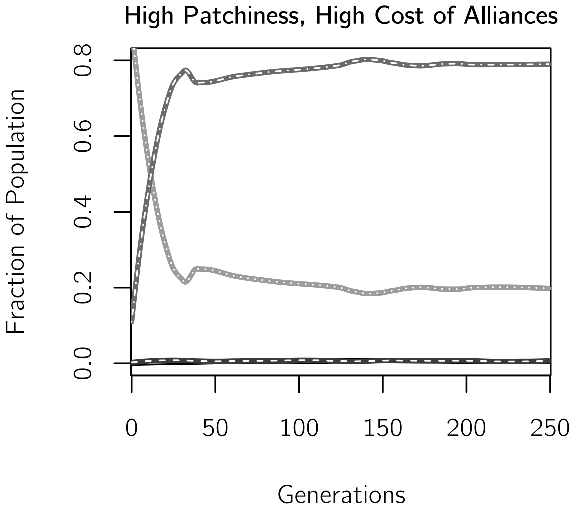
Environment B is marked by a highly patchy distribution of resources across the landscape (the landscape in the third row, middle column of Figure 2). Despite the initial nonterritorial starting point, mutant territorial strategies quickly come to dominate the population. Because environment B has relatively high costs of cooperation, enforcement, and hierarchy, solitary territorial strategies win out over alliance-forming strategies. Environment C has the same patchiness as B, but with relatively lower costs of cooperation and high costs of enforcement and hierarchy. In this context, alliance-forming territorial strategies outcompete solitary territorial strategies. Because hierarchy is relatively costly, however, non-hierarchical agents still outcompete hierarchical strategies.

Environment D has the same patchy landscape as B and C, but with relatively lower costs of cooperation and enforcement, and more efficient selection of leaders. After the initial establishment of territorial and alliance-forming strategies, hierarchical territorial agents come to dominate the landscape. Other territorial and

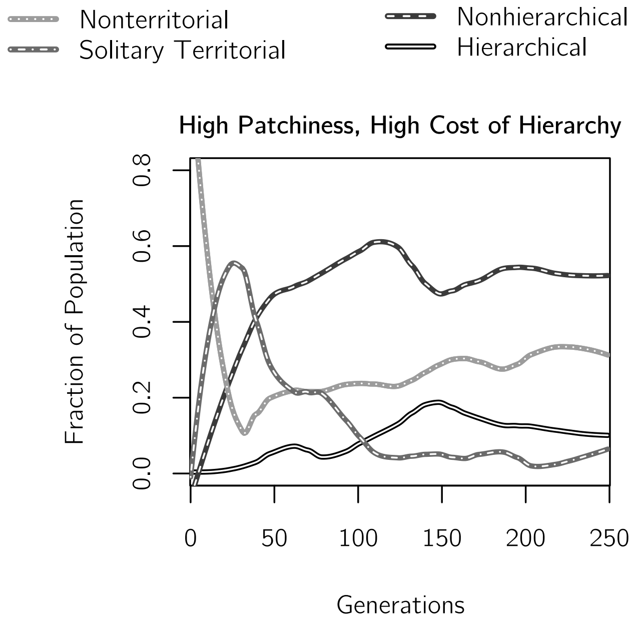
FIGURE 3 What favors the emergence of hierarchy? For all runs, $S = 0.2$, $\alpha = 4$, and $r = 0.36$. Lines were smoothed by local polynomial regression with loess smoothing parameter 0.3 (R Development Core Team 2008).



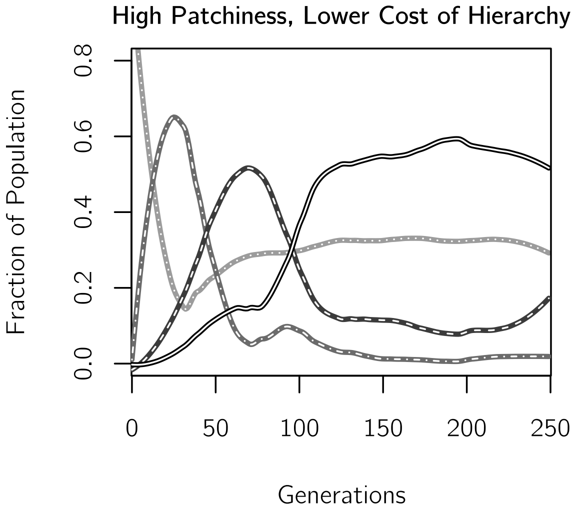
(A) An environment with low patchiness (i.e. low variance in the productivity of land, var(μ_k) = 0.005) yet low social costs of alliances and hierarchy ($c^A = 0.05$, $c^C = 0.05$, $c^E = 0.05$, $d = 1$). Nonterritorial agents outcompete territorial strategies and maintain predominance in the population.



(B) An environment with high patchiness (var(μ_k) = 0.055) and relatively high social costs of alliances and hierarchy ($c^A = 0.25$, $c^C = 0.35$, $c^E = 0.35$, $d = 1$). Solitary territorial agents quickly establish a majority in the population.



(C) An environment with high patchiness (var(μ_k) = 0.055), low costs of alliances (c^A = 0.05, c^C = 0.05), and high costs of hierarchy (c^E = 0.35, d = 1). Following an initial invasion of solitary territorial agents, non-hierarchical alliance-forming territorial agents form the majority of the population over time.



(D) An environment with high patchiness (var(μ_k) = 0.055) and relatively low costs of alliances and hierarchy (c^A = 0.05, c^C = 0.05, c^E = 0.05, d = 1). After initial invasions by solitary and alliance-forming territorial agents, hierarchical strategies dominate the population.

nonterritorial strategies are maintained in the minority through frequency-dependent selection.

The relationship between alliance size and strategy frequencies across ecologies can be summarized in three points. First, there is a general tendency for the size of alliances between territorial agents to first increase through time, then level off in dynamic equilibrium. Second, the long-run size of alliances varies across ecologies, with smaller groups in ecologies A and B, larger groups in ecology C, and the largest groups in ecology D. Third, hierarchical strategies consistently maintain larger alliances than nonhierarchical alliance-forming strategies. Hierarchy evolves in the context of and reinforces large territorial alliances

LONG-RUN OUTCOMES

The effects of patchiness and social costs of hierarchy on the long-run frequency of different strategies is illustrated in Figure 4. Territoriality always increases (while nonterritoriality decreases) with greater patchiness. Whether nonhierarchical or hierarchical territorial strategies are favored depends crucially on the costs of alliances and hierarchy. Hierarchical territorial strategies become common only when the costs of alliances and hierarchy are not prohibitively high.

The statistical analysis of long-run outcomes indicates that the effects of social parameters (the costs of alliances, cooperation, and enforcement and the decisiveness of alliances) on sociopolitical outcomes depend crucially on the underlying degree of patchiness (see Appendix, p. 306). In landscapes with greater patchiness, there are negative effects of the costs of alliance formation and the costs of cooperation on the frequency of territorial, alliance-forming, and hierarchical strategies. These effects are absent or muted in landscapes with low patchiness.

In patchier environments, the decisiveness of alliances drives

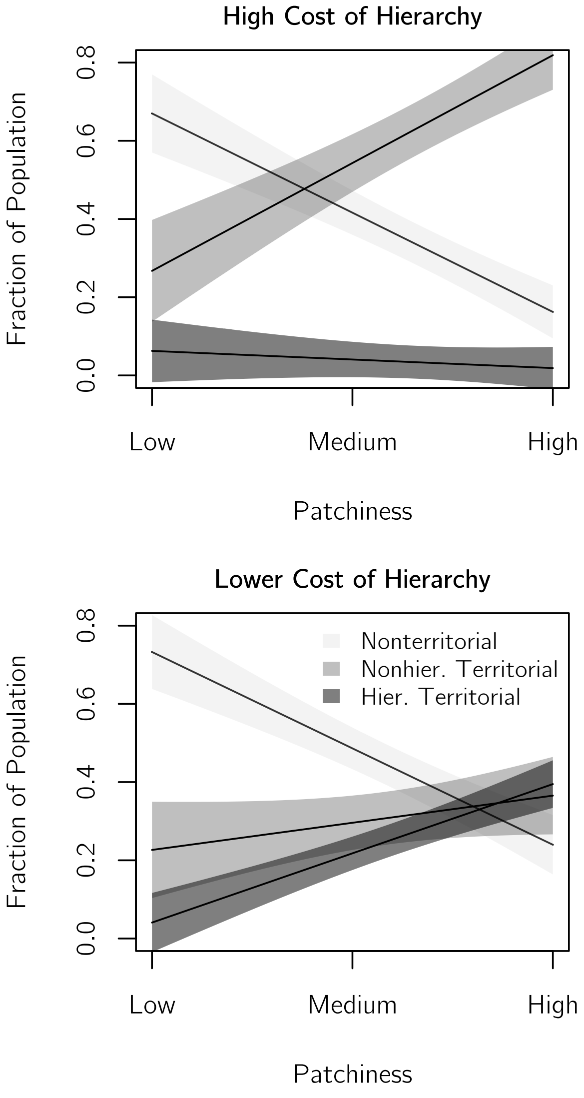


FIGURE 4 How do patchiness and the cost of hierarchy affect the evolution of territorial and hierarchical strategies? In both panels, increased patchiness results in fewer nonterritorial and more territorial strategies in the long run. Panel (A): When alliances and hierarchy are more costly ($c^A = 0.35$, $c^C = 0.35$, $c^E = 0.35$, $d = 0$), hierarchical strategies are always outcompeted by nonhierarchical strategies. Panel (B): When alliances and hierarchy are relatively less costly ($c^A = 0.05$, $c^C = 0.05$, $c^E = 0.05$, $d = 1$), hierarchical strategies become common at higher levels of patchiness. In both panels, $S = 0.2$, $\alpha = 4$, and $r = 0.36$. Lines and shading indicate predicted mean values and 95% confidence intervals from linear regression models estimating strategy frequencies after 250 generations.

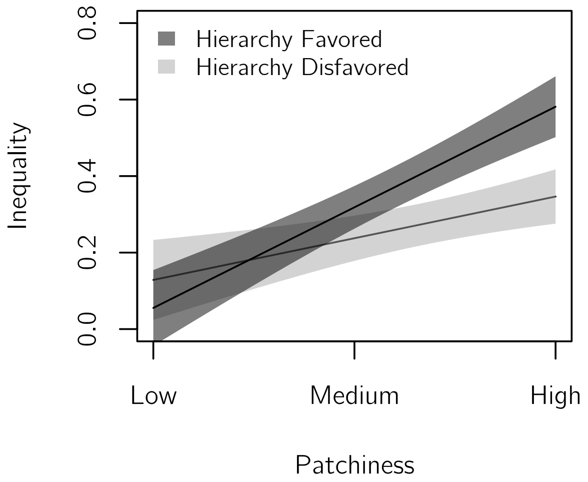


FIGURE 5 How do patchiness and hierarchy affect inequality? Inequality increases with patchiness in all environments. Patchiness leads to even greater inequality under conditions that favor the evolution of hierarchy (dark gray: $c^A = 0.05$, $c^C = 0.05$, $c^E = 0.05$, $d = 1$) compared to conditions that do not favor hierarchy (light gray: $c^A = 0.35$, $c^C = 0.35$, $c^E = 0.35$, $d = 0$). For both lines, $S = 0.2$, $\alpha = 4$, and $r = 0.36$. Lines and shading indicate predicted mean values and 95% confidence intervals from linear regression models estimating the Gini coefficient of fitness, Gini(W), after 250 generations.

higher frequencies of alliance–forming and hierarchical strategies. In very patchy landscapes, there are negative effects of the costs of enforcement on alliance-forming and hierarchical strategies, and positive effects of the efficiency of political processes in hierarchical groups on the frequency of hierarchical preferences.

The statistical analysis (see Appendix, p. 306) confirms the previous insight that the long-run size of alliances increases with landscape patchiness. Social and ecological parameters interact to determine alliance size: in patchier environments, alliance size increases with greater decisiveness of alliances, and decreases with the costs of alliance formation, cooperation, and enforcement. The results confirm that alliances grow to larger scales when the benefits (in terms of access to land) are high, and the social costs of alliance formation are not prohibitive. At very large scales, hierarchical alliances outcompete nonhierarchical alliances due to their efficiency in organizing for collective action in territorial competition.

Inequality is inextricably linked to hierarchy across the worlds simulated in this model, as shown in Figure 5. While hierarchical institutions grow in the context of high patchiness and inequality, they also amplify inequalities. In this simulation, hierarchy increases the Gini by roughly 50 percent, on top of the direct effects of patchiness and territoriality. This would not be the case if members of hierarchies could always choose the most efficient leaders at zero cost (Hooper et al. 2010).

Conclusions

The ecological and social dynamics that drive this model may be fundamental to the history of social hierarchy in our species. The model shows that hierarchy and inequality develop regularly in ecologies that favor the formation of coalitions to defend and contest resources.

Hierarchies for competition over resources are particularly likely where egalitarian means of promoting cooperation in coalitions are ineffectual and hierarchies are not unbearably costly. Hierarchies become more costly when group members are restricted in their ability to choose efficient leaders. In the real world, as in the model, hierarchical institutions that are inefficient relative to other feasible social arrangements often face overthrow, reform, or extinction. The difficulty and cost of these transitions, however, allows persistence of the kind of oppressive hierarchies observed countless times throughout history.

The model illustrates the interaction of ecological and social dynamics in two senses. First, the analysis shows the statistical interaction between ecology—in terms of the variance of land productivity—and other socioecological parameters, such as the cost of social interactions and the decisiveness of contests (see table in Appendix, p. 306). Second, the endogenous social dynamics are the very mechanism by which the effects of the exogenous ecological parameters are manifest through time (Figure 3); conversely, the effects of the social dynamics necessarily depend on the presence of favorable socioecological conditions. Thus, neither natural ecology nor social behavior alone is sufficient to explain the central result of the model: the emergence of norms and institutions for collective action, including hierarchy, in the presence of concentrated and predictable resources.

We have employed a definition of socioecology as the relationship between an organism and its natural, constructed, and social environments (Steward 1955; Winterhalder and Smith 2000; Odling-Smee et al. 2003; Kappeler et al. 2003). Technologies of production and competition therefore play important roles in driving transitions and shaping dynamic equilibria.

At very large scales, hierarchical alliances outcompete nonhierarchical alliances due to their efficiency in organizing for collective action in territorial competition.

A shift to reliance on high-quality agricultural land in the Holocene is likely to have increased the effective variance (patchiness) in the productivity of sites, increasing territoriality, alliance formation, and hierarchical territorial alliances. In other words, intensive agriculture transformed the economic value of territorial resources and created the crucible that produced the chiefdoms and states characteristic of the middle and later Holocene. Sedentism and higher population densities may have also reduced the costs of alliance formation, enforcement, and cooperation in ways that reinforced these outcomes. Mobile foragers relying on widely or unpredictably distributed plant and animal resources, on the other hand, have been less likely to go down this road to increasing sociopolitical complexity.

The dynamics and outcomes this model bear analogy with the depictions of Leach's *Political Systems of Highland Burma* (1973) and Scott's *The Art of Not Being Governed* (2010). In light of the empirical patterns Leach and Scott describe in Southeast Asia, the four environments in Figure 3 could be stylistically interpreted as: (A) and (B) inter-riverine forest tracts utilized by relatively egalitarian and acephalous foragers and farmers; (C) highland valleys suitable for shifting cultivation and agriculture inhabited by a mix of anarchic and hierarchical communities; and (D) productive alluvial valleys dominated by intensive agriculture and large-scale hierarchical polities.

In the Mississippian southeast, fortified villages cultivated crops on well-drained, sandy loam soils that were regularly renewed by inundation. Hudson (1976) proposed that once the best riverine soils came under cultivation, communities became environmentally circumscribed and joined together "beneath the mantle of a chief powerful enough to effect harmony... [and] to stand more strongly against mutual outside foes." The scale of integration and extent of sociopolitical complexity appear to have waxed and waned with the productivity and spatial extent of contiguous arable land (Munoz et al. 2015).

The development of the Northwest Coast hierarchical complex appears to have required millennia (Ames 1994; Matson and Coupland 1994), suggesting relatively slow rates of accumulation of the cultural traits required for the development of coherent hierarchies. Rapid social transitions following the introduction of new resources, technologies, or cultural models are also common in distant and recent history. Small-scale communities confronted by colonization and acculturation in the last 500 years have often moved toward more hierarchical and unequal social structures (Steward 1938; Hämäläinen 2009) and subordination to imperial or national hierarchies (Lee and Daly 2004; Hooper et al. 2014).

Contrary examples of reductions in hierarchy are also well documented (Currie et al. 2010; Scott 2010). Contemporary groups such as the Sungusungu of East Africa and the Kuna of Panama appear to gain from the complementarities between hierarchical organization and practices that limit the ability of leaders to advance personal gain over community interests (Paciotti and Borgerhoff Mulder 2004; Howe 2002; Kim Hill, personal communication). The theory predicts that hierarchical institutions provide the greatest benefits for their constituents when they coevolve with behaviors limiting their power and cost (Bowles 2012). Hierarchical institutions are constrained and can be replaced when less hierarchical forms of organization efficiently provide the same functions.

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