# Ecological and Social Dynamics of Territoriality and Hierarchy Formation

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**SANTA FE INSTITUTE**

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Paul L. Hooper[1],

Eric Alden Smith[2], Timothy A. Kohler[1,3],

Henry T. Wright[1,4] and Hillard S. Kaplan[1,5]

[1]Santa Fe Institute,
[2]University of Washington, [3]Washington State University Pullman,
[4]University of Michigan, and [5]University of New Mexico

## I. Introduction

The origins of complex societies fascinate us: societies with hierarchically organized political systems, specialized divisions of labor, and relatively unequal distributions of power and wealth. 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 92-98% 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 long-standing 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 America, multi-village political units encompassing 100-10,000 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 (Gunter 1972, Ames 1994, Matson & 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 (II) describe the model, (III) summarize its results, then (IV) discuss the implications for understanding hierarchy and state formation in human history.

## II. 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 (i) territorially defend sites, (ii) form territorial alliances, and (iii) establish territorial political hierarchies (Figure 1 and Table 1). The exogenous parameters of the 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 non-hierarchical alternatives.
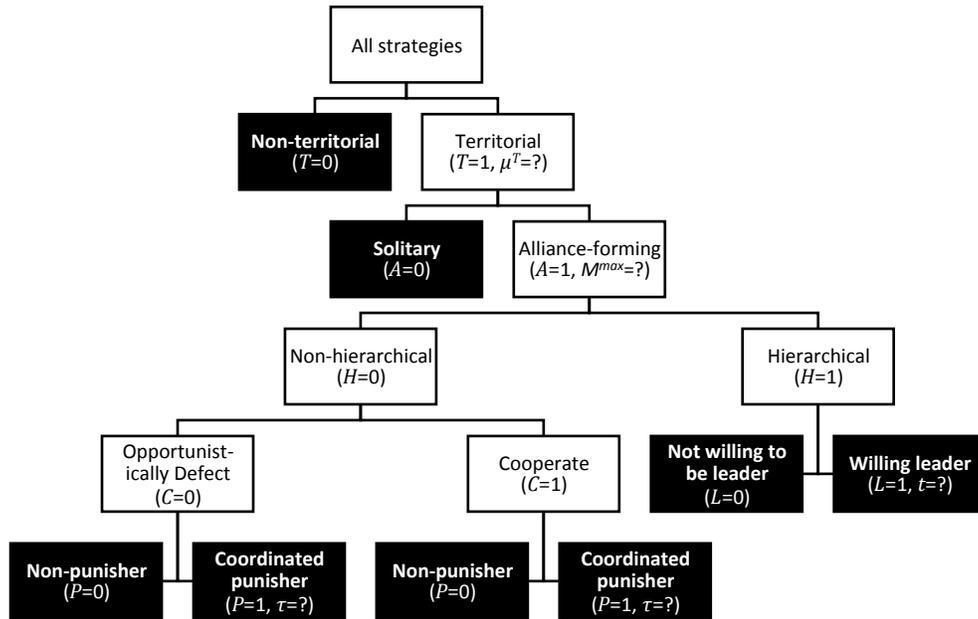


Figure 1. A nested taxonomy of strategy types. The black (terminal) nodes indicate fully specified strategy types.

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 | $\mu_i^T$ | 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 | $\tau_i$ | 0—N |
| Hierarchical | $H_i$ | 0, 1 | - | - | - |
| Willing leader | $L_i$ | 0, 1 | Tax offered as leader | $t_i$ | 0—∞ |

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 & Choi 2007, Hooper et al. 2010, Boyd et al. 2010). The model nests the strategies and replicator dynamics of evolutionary game theory (McElreath & 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 re-create 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.

Table 2. Exogenous socioecological parameters.

| | *Parameter* | *Symbol* | *Values* |
|---|---|---|---|
| Focal | Variance in patch productivity | $\mathrm{var}(\mu_k)$ | 0.005, 0.030, 0.055 |
| | Decisiveness of alliances | $\alpha$ | 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) | $w \times w$ | 33 × 33 |
| | Mean patch productivity | $\mathrm{mean}(\mu_k)$ | 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 $\mu$; ★ In units of $w$.

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 $\geq 1$ willing punishers in $i$'s alliance | $\hat{P}(1)$ | 0, 1 |
| There are $\geq \tau_i$ willing punishers in $i$'s alliance | $\hat{P}(\tau_i)$ | 0, 1 |
| Number of followers of $i$ | $F_i$ | 0—$N$ |

The spatial landscape of the model is defined as a $w \times w$ torus containing $w^2$ patches. In each round, each patch $k$ produces one resource unit (productivity $L_k = 1$) with probability $\mu_k$, and produces nothing ($L_k = 0$) with probability $1-\mu_k$. The spatial distribution of mean productivity $\mu_k$ (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 $\mu_k$ (Figure 2). These landscapes have the same overall mean productivity of patches $\bar{\mu}$, but different values for both the "patchiness" of the landscape (i.e. variance in productivity across patches: var($\mu_k$)), 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 $\Phi$ ($0 < \Phi < 20$), then renormalized to achieve the target values of $\bar{\mu}$ and var($\mu_k$). 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 re-interpreted in terms of temporal variability (or predictability), with some important differences discussed in Dyson-Hudson & Smith (1978).
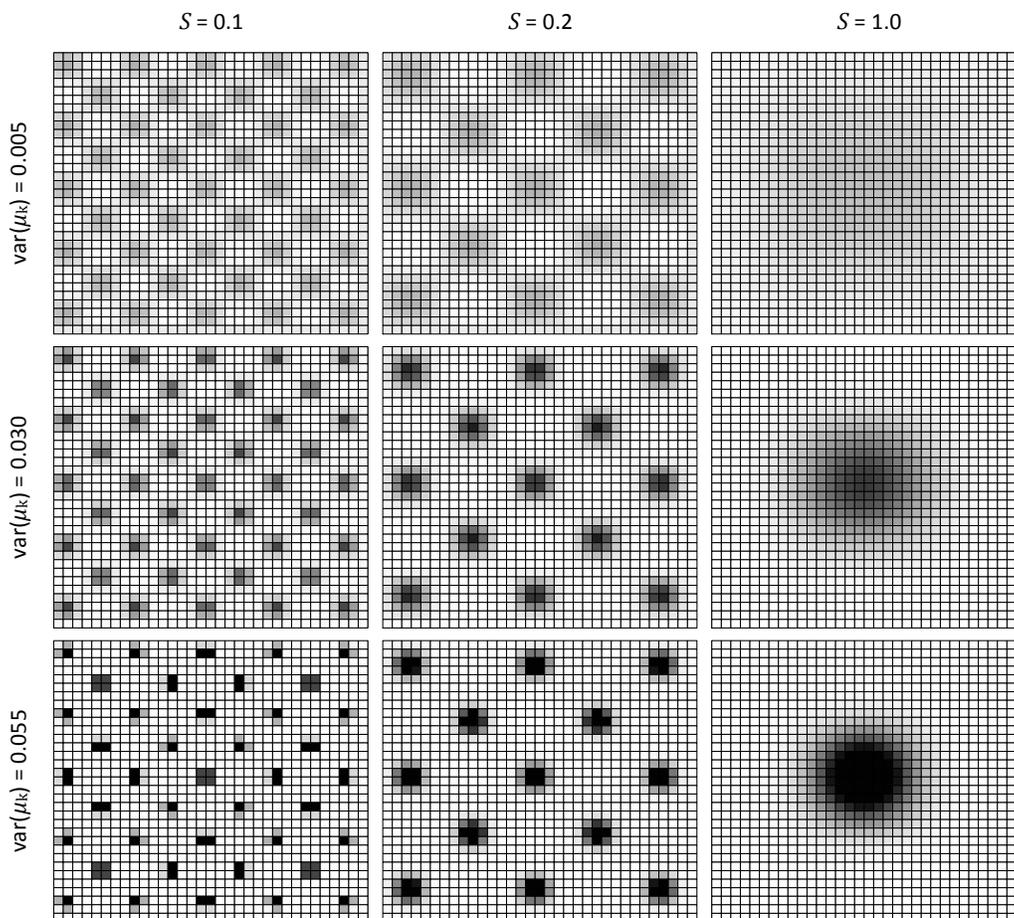


Figure 2. Nine ecologies differing in patchiness, var($\mu_k$), and spatial clustering of productive patches, $S$. Patchiness increases from top to bottom, while clustering increases from left to right. The mean productivity of each landscape, mean($\mu_k$), is held constant at 0.1.

## Strategies and interaction

The landscape is seeded with a small number of non-territorial agents, interpretable as single individuals or family units. In each non-overlapping generation, agents interact over multiple rounds (default = 25). In each round, in random order, each agent attempts to move onto 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 employs either a non-territorial strategy ($T_i = 0$) or a territorial strategy ($T_i = 1$). Non-territorial 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 $k$). Non-territorial agents are thus facultatively nomadic, moving when productivity can be improved, and staying when local productivity remains high.

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 of the patch. The strength of an agent in contesting a patch $\sigma_i$ depends on whether it employs a solitary strategy ($A_i = 0$) or 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 the 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. Non-hierarchical agents ($H_i = 0$) form alliances with other non-hierarchical 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 alliance-forming agent $j$ within $i$'s spatial reach who is not already claiming a patch, has fewer than $M_j^{max}$ alliance partners, and is able to find a patch adjacent to the patch targeted by $i$ that is above its contest threshold $\mu_j^T$, 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 $\sigma_i$ 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 non-hierarchical 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 at least $\tau$ coordinated punishers present in the alliance, where $\tau$ 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 $M^P$ 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 is selected that offers the lowest tax; when $d = 0$, the leader is selected offering the highest tax; 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 non-hierarchical alliance, in which cooperation either remains unenforced or is enforced through coordinated punishment.

At the end of each round, the resources produced by each patch are divided equally among and its occupants and added to their cumulative lifetime fitness. The per-round contribution to fitness of individual $i$ occupying patch $k$ (equation 1) is thus equal to the per capita productivity of patch $k$ (1st term: $L_k/N_k$) minus the costs of their strategy- and context-dependent behavior: the costs of maintaining alliances (2nd term: $c^A M_i$); the cost of cooperating to defend territory, whether dictated by strategy or stimulated by enforcement (3rd term: $c^C \max(C_i, H_i, \hat{P}(1))$); the coordinated punisher's cost of enforcing the cooperation of each opportunistic defector (4th term: $c^E \hat{P}(\tau_i) M_i^D/M_i^P$); and the hierarchical agent's cost of being taxed (5th term: $t_j H_i$). Hierarchical agents that enforce cooperation as leaders also receive the benefit of taxation minus the cost of enforcement for each of $F_i$ followers (6th term: $(t_i - c^E M_i^D/M_i)F_i$). The individual's per-round contribution to fitness $w_i$ is defined by Equation (1):

$$w_i = L_k/N_k - c^A M_i - c^C \max\left(C_i, H_i, \hat{P}(1)\right) - \hat{P}(\tau_i)c^E M_i^D/M_i^P - t_j H_i + \left(t_i - c^E M_i^D/M_i\right)F_i \quad (1)$$

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 $\alpha$ in this expression represents the decisiveness of alliances in determining the outcome of contests. When $\alpha$ is greater, the slope of the S-shape curve around the inflection point (where the two alliances are of equal strength) is steeper, reflecting more of a winner-take-all environment. $\alpha$ thus reflects how important the relative size of the alliance is 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 claims new patches remain linked as allies once they have settled on their new territory. Members of defensive alliances that are not ejected from the patches they claim also remain linked as allies following the contest.

*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: $W_i = B\overline{w}_i$. 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 $\mu_i^T$ 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 $\tau_i$ 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 principle outcomes of the model, as they evolve through time (Figure 3) and after a long period of evolution (Table 4).

To produce the historical trajectories plotted in Figure 3, five runs of 250 generations playing 25 rounds per generation were simulated in each of three contrasting socioecologies: (A) an ecology with low landscape patchiness, low costs of cooperation and enforcement, and efficient political institutions; (B) an ecology with high landscape patchiness, high costs of cooperation and enforcement, and inefficient political institutions; and (C) an ecology with high landscape patchiness, low costs of cooperation and enforcement, and efficient political institutions. Local polynomial regression was used to characterize the mean frequency of each strategy and group size as a function of time (using the loess function in R; R Development Core Team 2008).

For the statistical analysis of long-run outcomes summarized in Table 4, 200 runs of 250 generations playing 25 rounds per generation were parameterized by randomly sampling the parameter values given in Table 2. For each parameter (with the exception of landscape patchiness) one of three values was sampled with equal probability. For the landscape patchiness, $var(\mu_k)$, 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 and mean alliance sizes were estimated as a function of socioecological parameters in a multi-level, mixed-effects regression using the lmer function in the lme4 package in R (Bates et al. 2013). The sample for the regression includes one observation for each of the last 100 generations of each run, with a random effect term to capture the non-independence of outcomes within each run. Inequality—measured by the gini coefficient of fitness, $gini(W)$, in the last generation of each run (using the reldist package; Handcock 2015)—was estimated as a function of socioecological parameters using the lm function.

The models includes main effects for the low-, medium-, and high-patchiness conditions, and the interaction of these conditions with other key socioecological parameters: the decisiveness of alliances in determining contests $\alpha$; the cost of allies $c^A$; the cost of cooperation $c^C$; the cost of enforcing cooperation $c^E$; and the efficiency of political processes selecting leaders $d$. The continuous predictor and response variables (except for the gini) were normalized to have mean 0 and standard deviation 1. The reported standardized regression coefficients ($\beta$s) thus indicate a change of $\beta$ standard deviations in the response variable with an increase of 1 standard deviation in the predictor variable.

## III. Results

The effects of social and ecological parameters on the population dynamics of non-territorial and territorial agents are illustrated across panels A, B and C in Figure 3. Environment A is characterized by a relatively homogeneous distribution of productivity across the landscape (the landscape in the 1st row, middle column of Figure 2). In this environment, non-territorial agents retain the advantage over territorial strategies, maintaining a long-run mean of around 2/3rd of the population.

Environment B is marked by a highly patchy distribution of resources across the landscape (the landscape in the 3rd row, middle column of Figure 2). Despite the initial non-territorial starting point, mutant territorial strategies quickly come to dominate the population. Because this is an environment with relatively high costs of cooperation and enforcement and inefficient selection of leaders, however, non-hierarchical territorial strategies win out over hierarchical agents.
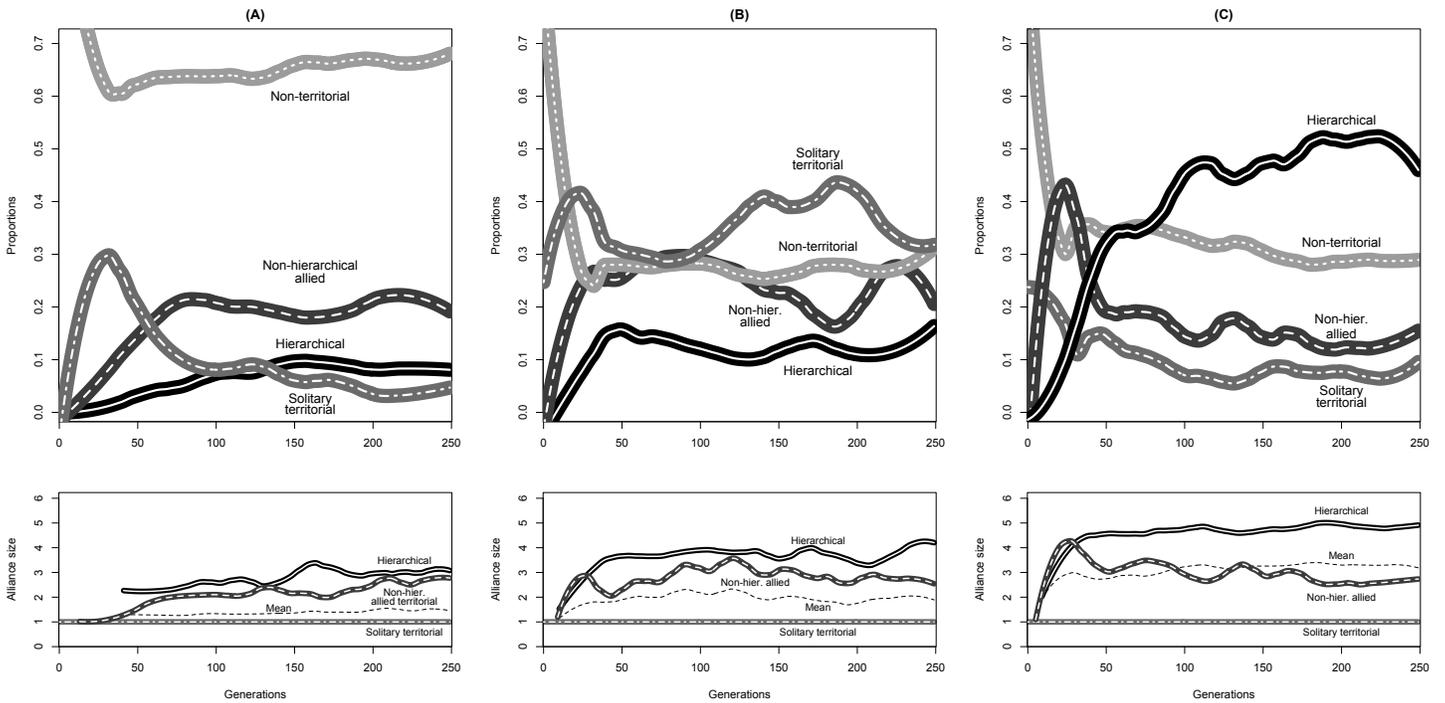
Figure 3. Engine of history. Mean frequencies (top row) and alliance sizes (bottom row) of non-territorial, solitary territorial, non-hierarchical alliance-forming, and hierarchical strategies through time. Panel (A): An environment with low variance in land productivity (var($\mu_k$)=0.005, $c^C$=0.05, $c^E$=0.05, $d$=1). Panel (B): An environment with high variance in land productivity, but high costs of hierarchy (var($\mu_k$)=0.055, $c^C$=0.35, $c^E$=0.35, $d$=0). Panel (C): An environment with high variance in land productivity and relatively low costs of hierarchy (var($\mu_k$)=0.055, $c^C$=0.05, $c^E$=0.05, $d$=1). For all runs, $S$=0.2, $\alpha$=4, $c^A$=0.05, and $r$=0.36. Each line shows a local polynomial regression fit over 5 runs with loess smoothing parameter 0.3.

Environment C has the same patchy landscape as B, 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 non-territorial strategies are maintained in the minority through frequency-dependent selection.

The relationship between alliance size and strategy frequencies across ecologies is observable in the bottom panels of Figure 3. Three main features of these trajectories are important. First, there is a tendency in all three ecologies 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 mean group sizes increasing from ecology A to B to C. Third, hierarchical strategies consistently maintain larger alliances that non-hierarchical alliance-forming strategies. The extent of this difference, moreover, increases under conditions favorable for hierarchy.

The statistical analysis in Table 4 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. 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.

Table 4. Predicted effects of socioecology on strategy frequencies, alliance size, and inequality given low, medium, and high patchiness.

| Landscape patchiness var($\mu_k$) | Parameter | | Strategy frequencies | | | | | | Mean alliance size | Inequality gini($W$) |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Non-territorial $\beta$ | Territorial $\beta$ | Alliance-forming $\beta$ | Cooperative $\beta$ | Coordin'd punisher $\beta$ | Hierarchical $\beta$ | $\beta$ | $\beta$ |
| Low | (Intercept) | - | 1.35 *** | -1.35 *** | -0.06 | 0.43 *** | 0.97 *** | -0.22 * | -0.57 *** | 0.10 *** |
| | Decisiveness of alliances | $\log(\alpha)$ | -0.02 | 0.02 | 0.05 | 0.03 | 0.13 | 0.03 | -0.06 | 0.01 |
| | Cost of ally | $c^A$ | -0.07 . | 0.07 . | 0.02 | -0.01 | 0.10 | 0.02 | -0.05 | 0.01 |
| | Cost of cooperation | $c^C$ | -0.10 * | 0.10 * | 0.05 | 0.10 | 0.13 | 0.04 | -0.05 | 0.01 |
| | Cost of enforcement | $c^E$ | -0.05 | 0.05 | 0.04 | -0.02 | 0.06 | 0.01 | -0.03 | 0.01 |
| | Effic. of political process | $d$ | 0.06 | -0.06 | -0.07 | -0.13 | -0.33 * | -0.03 | 0.09 | 0.00 |
| Medium | (Intercept) | - | -0.27 *** | 0.27 *** | -0.15 | -0.43 *** | -0.20 | -0.02 | 0.10 | 0.23 *** |
| | Decisiveness of alliances | $\log(\alpha)$ | -0.01 | 0.01 | 0.16 . | 0.03 | 0.08 | 0.23 * | 0.20 * | 0.01 |
| | Cost of ally | $c^A$ | -0.03 | 0.03 | -0.73 *** | -0.04 | -0.22 . | -0.27 * | -0.54 *** | -0.02 |
| | Cost of cooperation | $c^C$ | -0.04 | 0.04 | -0.40 *** | -0.09 | 0.03 | -0.69 *** | -0.49 *** | -0.01 |
| | Cost of enforcement | $c^E$ | -0.04 | 0.04 | 0.06 | 0.01 | -0.04 | 0.04 | 0.03 | 0.01 |
| | Effic. of political process | $d$ | -0.03 | 0.03 | -0.07 | 0.02 | -0.02 | 0.05 | 0.00 | 0.01 |
| High | (Intercept) | - | -0.72 *** | 0.72 *** | 0.26 *** | -0.36 *** | -0.16 . | 0.32 *** | 0.44 *** | 0.33 *** |
| | Decisiveness of alliances | $\log(\alpha)$ | 0.01 | -0.01 | 0.18 ** | 0.07 | 0.01 | 0.28 *** | 0.13 . | 0.06 *** |
| | Cost of ally | $c^A$ | -0.10 ** | 0.10 ** | -0.82 *** | -0.04 | -0.24 ** | -0.45 *** | -0.75 *** | -0.03 * |
| | Cost of cooperation | $c^C$ | -0.06 * | 0.06 * | -0.29 *** | -0.16 ** | -0.06 | -0.69 *** | -0.21 ** | -0.05 *** |
| | Cost of enforcement | $c^E$ | -0.04 | 0.04 | -0.13 . | 0.00 | -0.01 | -0.13 . | -0.16 * | -0.05 *** |
| | Effic. of political process | $d$ | -0.02 | 0.02 | 0.00 | 0.01 | 0.02 | 0.13 . | 0.02 | 0.01 |

Notes: $n$ = 20,000 generations in 200 runs for each model (with random effects for run), except for inequality, where $n$ = 200 runs (without random effects). *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; . $p < 0.1$.

In patchier environments, the decisiveness of alliances drives 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.

Table 4 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 non-hierarchical alliances due to their efficiency in organizing for collective action in territorial competition.*

Relationships between socioecology and inequality (represented as the gini coefficient of fitness) are given in the final right-hand column of Table 4. Like territoriality and hierarchy, inequality increases with patchier distributions of resources. In the patchiest environments, inequality depends on those parameters underlying territoriality, alliance-formation, and hierarchy: high decisiveness of alliances and low costs of cooperation and enforcement.

Inequality is inextricably linked to hierarchy across the worlds simulated in this model. 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%, 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).

**IV. 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 individuals are restricted in their ability to choose efficient leaders (and other members of the hierarchy). 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 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 para-meters, such as the cost of social interactions and the decisiveness of contests (Table 4). 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 & 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.

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 (1973) *Political Systems of Highland Burma* and Scott's (2010) *The Art of Not Being Governed*. In light of the empirical patterns they describe in Southeast Asia, the three environments in Figure 3 could be stylistically interpreted as: (A) inter-riverine forest tracts utilized by relatively egalitarian and acephalous foragers and farmers; (B) highland valleys suitable for shifting cultivation and agriculture inhabited by a mix of anarchic and hierarchical communities; and (C) 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 appears 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 & 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 half millennium 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 & Borgerhoff Mulder 2004, Howe 2002, Kim Hill, personal communication). The theory predicts that hierarchical institutions provide the greatest benefits for their constituents when they co-evolve 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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