Ecological variation and institutionalized inequality in hunter-gatherer societies

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Research examining institutionalized hierarchy tends to focus on chiefdoms and states, while its emergence among small-scale societies remains poorly understood. Here, we test multiple hypotheses for institutionalized hierarchy, using environmental and social data on 89 hunter-gatherer societies along the Pacific coast of North America. We utilize statistical models capable of identifying the main correlates of sustained political and economic inequality, while controlling for historical and spatial dependence. Our results indicate that the most important predictors relate to spatiotemporal distribution of resources. Specifically, higher reliance on and ownership of clumped aquatic (primarily salmon) versus wild plant resources is associated with greater political-economic inequality, measuring the latter as a composite of internal social ranking, unequal access to food resources, and presence of slavery. Variables indexing population pressure, scalar stress, and intergroup conflict exhibit little or no correlation with variation in inequality. These results are consistent with models positing that hierarchy will emerge when individuals or coalitions (e.g., kin groups) control access to economically defensible, highly clumped resource patches, and use this control to extract benefits from subordinates, such as productive labor and political allegiance in a patron–client system. This evolutionary ecological explanation might illuminate how and why institutionalized hierarchy emerges among many small-scale societies.

evolutionary ecology | hierarchy | economic defensibility | patron-client systems

Explaining the origins of institutionalized hierarchy, involving hereditary inequality in wealth and power, remains contentious. Evidence suggests that such institutions arose and spread relatively recently, in the last 10 to 11 millennia (1, 2), despite the fact that modern humans evolved at least 200 millennia ago (3, 4). Although large-scale, highly stratified state systems arose only in the context of intensive agriculture, evidence shows that reliance on domesticated crops is neither necessary nor sufficient to generate institutionalized inequality at smaller scales. A number of widely scattered hunter-gatherer societies exhibit hereditary inequality (5–7), while many horticulturalist societies with shifting agriculture lack such institutions (8). Furthermore, in contrast with other primates, inequality in small-scale human societies is not primarily a result of coercion or dominance relations (9, 10). What then favors the emergence and persistence of inequality in some small-scale societies?

Drawing on current models that seek to explain social hierarchy, this paper analyzes the variation in institutionalized inequality among Indigenous (Native American) societies of the Pacific coast of North America, from what is now southern California to southeast Alaska. Although this region lacked any reliance on domesticated crops or animals, it exhibited substantial variation in inequality. Some societies, primarily along the North Pacific coast, were characterized by a class system of hereditary nobility, commoners, and slaves, with nobles directing the labor of commoners and slaves alike and controlling large stores of wealth (11, 12). Others, primarily in California, united a few small settlements under nonhereditary leaders with limited

power and wealth, and constituent households exercised considerable economic and political autonomy (13, 14). Ethnographers and archaeologists have long noted these contrasts and proposed various accounts of how they arose. Although earlier explanations positing resource abundance as driving Northwest Coast social complexity (15) have not held up well, the systematic variation along the coast noted by many scholars (16–18) has sparked a number of recent syntheses (refs. 6, 11, 12, 14, among others).

We test several alternative explanations for variation in the degree of inequality in Native California and the Northwest Coast. In line with current theory, these hypotheses variously emphasize demographic (population scale, Malthusian pressure), ecological (environmental productivity, spatiotemporal distribution of key resources), and competitive (armed conflict, control of resource patches) variables as predictors or "drivers" of hierarchy and inequality. To the degree possible, we focus on ethnographic reconstructions of societies at or shortly following contact with Europeans or Euroamericans, as well as relevant environmental data, to describe and analyze the patterns of variation.

After outlining our theoretical framework and key hypotheses, we use statistical models from machine learning and nonlinear regression to evaluate the degree to which each hypothesis accounts for the variation in inequality we seek to explain, while controlling for cultural (linguistic) phylogeny and spatial proximity. Details on the data sources, statistical methods, and the

Significance

Persistent differences in wealth and power are pervasive in contemporary societies, yet were absent or muted for most of human history. To help explain how and why institutionalized hierarchy can arise in egalitarian systems, we examine a sample of Native American hunting and gathering societies that vary in the degree of inequality. Systematic evaluation of alternative hypotheses identifies the presence of defensible clumped resources that can be monopolized as a likely determinant of institutionalized hierarchy. When such resources are present, societies in our study exhibit substantial inequality, including slavery. Other possible predictors, such as population pressure and warfare, do not show this effect. These results suggest general factors likely facilitate the initial emergence of inequality in human societies.

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operational measures used to test our hypotheses are described in the *Materials and Methods*.

Theoretical Framework and Key Hypotheses

Despite a long history of inquiry, there is little consensus on the key factors driving the emergence of institutionalized inequality in wealth and power in small-scale societies. Proposed drivers include population pressure, risk buffering, trade monopolies, spatially concentrated resources, military conflict, resource storage, control of production technology, scalar effects of increasing population density or community size, competitive feasting and gift-giving, and manipulation of social networks or ideology (3, 5, 19, 20). Formal models and simulations addressing the issue have recently proliferated (21–27). Rather than offer additional models, we draw on several extant ones to evaluate explanatory scenarios that are most amenable to empirical tests with the available data. These involve 1) population pressure (Malthusian constraints), 2) scalar effects of polity size or population density, 3) intergroup conflict, and 4) differential control of concentrated resource patches.

Population pressure explanations for the emergence of inequality, sociopolitical complexity, and related phenomena have a long and contentious history (3, 28). Although arguments vary, the typical version views per capita resource scarcity and resulting competition as motivating agents to adopt hierarchy in order to gain competitive advantage within or between groups. In a relatively empty habitat where resource supply exceeds demand, latecomers or less competitive individuals can disperse to unoccupied (but perhaps lower grade) habitats, and population/resource equilibrium will approximate an ideal-free distribution (29). However, in packed habitats, those with greater competitive ability might emerge as elites, imposing an ideal-despotic distribution (21, 30–32).

Some researchers point out that increased population, regardless of resource scarcity, creates exponential increases in social ties, posing problems of information management, social coordination, or internal conflict. These "scalar" stresses will lead to group fissioning, unless they can be countered by the emergence of higher-level integrative institutions. Theorists posit that this solution will entail some form of sociopolitical hierarchy (33–35).

Intergroup conflict is hypothesized to drive institutionalized hierarchy in several ways. Strong leadership could coordinate and enforce effective defense against enemy attacks and have similar advantages in the conduct of offensive raids (23, 36). In addition, hereditary inequality could develop if leaders of raiding parties can regularly assert control over plunder or captured slaves (36–38).

Control over productive resource sites is often proposed to drive emergence of hierarchy. Although there are various versions of this proposal, perhaps the best-developed scenario involves patron–client systems (27, 39). Although related to the ideal-despotic argument summarized above (40), this scenario focuses on internal social relations and unequal division of collective goods, as in models of reproductive skew (41–43). It posits that when key resources are sufficiently dense, predictable, and clumped, the richest resource patches can be successfully controlled by a subset of individuals within the social group (3, 44). These individuals can then use these claimed property rights to establish a system of patron–client relations, extracting benefits from subordinates up to the point the latter could do better by moving to another locale, joining another group, or actively contesting ownership (21, 23, 39, 45). The patron–client scenario thus requires not only economic defensibility (46) in the form of dense and spatiotemporally predictable resources (47) but also that key resources that are sufficiently clumped and differentiated into richer versus poorer patches, such that some individuals or factions (e.g., kin groups) can exchange access to them for

labor and other services—that is, develop patron–client systems (3, 23, 39).

In summary, we organize our analysis around four key hypotheses derived from the extant theoretical and empirical literature. These hypotheses in turn link to specific predictor variables (Table 1), as we describe below. Our primary source for ethnographic data on the 89 Northwest Coast and California societies is the Western North American Indian (WNAI) database (48, 49); additional demographic and newly generated environmental data are derived from other sources, as detailed in the *SI Appendix*. Our outcome measure for all hypotheses is a "Hierarchy Index" (HI) scoring the presence of three WNAI variables: unequal food distribution, ranking within kin groups, and slavery (see *Materials and Methods* and *SI Appendix*). The HI thus can vary from 0 to 3, and the full range is found across our 89 cases (Fig. 1 and *SI Appendix,* Fig. S1).

1. H1 proposes that population pressure (per capita resource scarcity) drives internal resource competition, favoring institutionalized inequality. We evaluate H1 using three measures of local resource availability, all converted to per capita values: annual fish harvest, proportion of territory occupied by oak (*Quercus* spp.) woodlands (this study, from ref. 50), and annual net primary productivity (this study, from ref. 51).

2. H2 proposes that scalar effects of population density or polity size create a demand for institutionalized leadership to handle increased conflict or coordination issues. To evaluate this hypothesis, we rely on estimates of local population density and polity size (*SI Appendix,* Table S1).

3. H3 focuses on intergroup conflict and posits that chronic raiding favors the emergence of leaders to enhance raiding success and/or through control of plunder. We test H3 using estimates of the frequency of offensive raiding and raiding for plunder.

4. H4 posits that control of highly clumped, productive resource patches allow subsets of social groups to trade access for labor contributions and surplus production. To evaluate H4, we rely on estimates of fish harvest per unit area, fishing site ownership, spatial dispersion (SD) of net primary productivity (*SI Appendix,* section A), and a Resource Index (RI) defined as the difference between reliance on aquatic resources and dietary percentages of the other two resource classes (gathered plants and terrestrial game). This index is designed to capture the relative reliance on more clumped and defensible resources and is mathematically equivalent to aquatic resource consumption (*SI Appendix,* section A).

Results

The theoretical arguments outlined above propose that one or more key factors will favor the development of contrasting patterns of political and economic inequality in small-scale societies. We begin with a global assessment of the array of ten variables nominated as drivers of inequality in the above hypotheses, plus three control variables (language family, latitude, and longitude) in a random forests machine learning model (see *Materials and Methods*). We then present a second independent test of each alternative hypothesis by constructing four competing generalized additive models (GAMs) to identify the most important predictors of institutionalized hierarchy in our data. The resulting variables are then assessed using a piecewise structural equation model (pSEM) in order to evaluate the direct effects of exogenous (i.e., environmental) variables on hierarchy as well as their indirect effects through endogenous (i.e., social) variables.

The random forests model including all ten theoretically derived predictors plus three control variables identifies only six as being important for predicting hierarchy: the RI, latitude, longitude, fishing site ownership, offensive raiding, and terrestrial

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Table 1. Variables employed in hypothesis evaluation

Variable	Role	Source
Annual per capita fish harvest	Predictor (H1)	WNAI p135/Local population (*SI Appendix*, Table S1)
Areal proportion in *Quercus* woodlands, per capita	Predictor (H1)	This study, from ref. 50
Annual per capita NPP	Predictor (H1)	This study, from ref. 51
Local population density	Predictor (H2)	*SI Appendix*, Table S1
Average polity size	Predictor (H2)	*SI Appendix*, Table S1
Offensive raiding frequency	Predictor (H3)	WNAI v361
Raiding for plunder	Predictor (H3)	WNAI d354
NPP spatial dispersion	Predictor (H4)	This study, *SI Appendix*, section A
RI (relative aquatic dietary %)	Predictor (H4)	WNAI p199 − (p204 + p211)
Fishing site ownership	Predictor (H4)	WNAI d271
HI	Outcome variable	Sum of WNAI d252, d318, and d436

environmental productivity per capita (Fig. 2 and *SI Appendix, Fig. S4*). The best model with only these six variables explains 86% of the variance in the HI. Cross-validation model evaluation reveals the median model prediction error is 0.26 ± 0.08 (*SI Appendix, Fig. S5*), indicating that the model accurately predicts the level of hierarchy within the observed level of hierarchy (i.e., is less than 0.5). Model residuals are normally distributed around zero (*SI Appendix, Fig. S6*) and do not contain significant spatial autocorrelation, but do include significant linguistic dependence (*SI Appendix*, section E), indicating that the effects of spatial proximity, but not language, are accounted for in the model. As shown in Fig. 2 (see also *SI Appendix, Fig. S7*), when holding all other variables constant, the RI (effect size [es] = 0.37) has the greatest effect on the HI, followed closely by latitude (es = 0.35). Longitude (es = −0.22) has the next greatest (though negative) effect, followed by fishing site ownership (es = 0.13). Finally, terrestrial environmental productivity per capita (es = 0.04) and offensive raiding (es = −0.01) have small effects that are an order of magnitude lower than the other variables. Partial response plots of the top four variables are shown in *SI Appendix, Fig. S7*. These results are most consistent with the patron–client hypothesis (H4) for the emergence of hierarchy.

A comparison of generalized additive models evaluating each theoretically derived hypothesis indicates that the H4 model outperforms all the others. It has the lowest Akaike Information Criterion (AIC) score and is the only model with significant predictor variables (Table 2 and *SI Appendix, Table S6*). Stepwise selection of the H4 variables indicates that a model including only the RI and fishing site ownership (plus controls) outperforms all the others by AIC (Table 2), and an analysis of deviance comparing each of the H4 model variants indicates that it is significantly better (P = 0.0150). This model is also better than a null model that includes only the control variables based on AIC (Table 2) and an analysis of deviance (*SI Appendix*, section E). This best model explains 71% of the deviance in the HI. The model residuals are normally distributed around zero (*SI Appendix, Fig. S8*) and do not contain significant spatial autocorrelation but do harbor linguistic autocorrelation (*SI Appendix*, section E). As shown in Fig. 3, the HI increases monotonically as a function of reliance on aquatic resources and is greater where fishing sites are owned.

A piecewise structural equation model confirms that both the RI (standardized coefficient [β_{std}] = 2.16, P < 0.0001) and fishing site ownership (β_{std} = 0.96, P = 0.043) have significant direct effects on hierarchy (Fig. 4). The RI has a positive, though not significant, indirect effect on hierarchy mediated through fishing site ownership (β_{std} = 0.70, P = 0.317). A model without a path linking RI and fishing site ownership further suggests that there is not a meaningful indirect effect of RI on hierarchy mediated through fishing site ownership (*SI Appendix*, section E).

Discussion

Our analysis suggests that variation in institutionalized inequality among 89 Indigenous North American societies of the Pacific Coast is best explained by the differences in subsistence ecology associated with the control over key resource patches. Specifically, we found a robust association between the importance of aquatic foods (the RI) and the ownership of fishing sites with a composite measure of political and economic inequality (the HI). We argue that the primary reason for this is that the key resources in northern areas (particularly runs of salmon and other fish such as spawning herring and eulachon) were dense, relatively predictable, and concentrated in space and time, allowing access to these resource patches to be controlled by a subset of individuals in each local group, typically members of the highest-ranking kin group headed by a hereditary chief. In contrast, key resources to the south (particularly acorns and other wild plant foods, as well as waterfowl, a wide variety of fish, and deer) were more evenly dispersed in space, and either available over broad parts of the year or else easily stored (as unprocessed nuts) until needed. As a consequence, in most of California, no individual, kin group, or faction could effectively monopolize rich resource
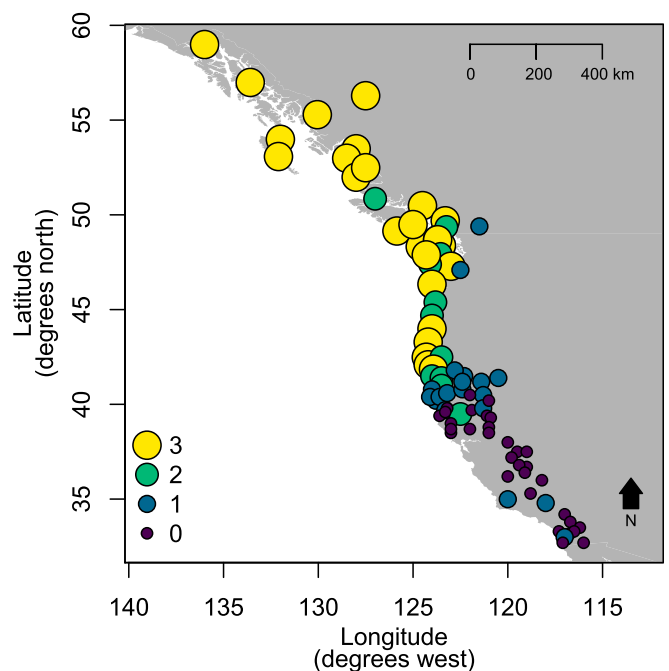

Fig. 1. Map illustrating the location of each society in this study, with the size and color of the dot indicating the degree of institutional hierarchy (HI).
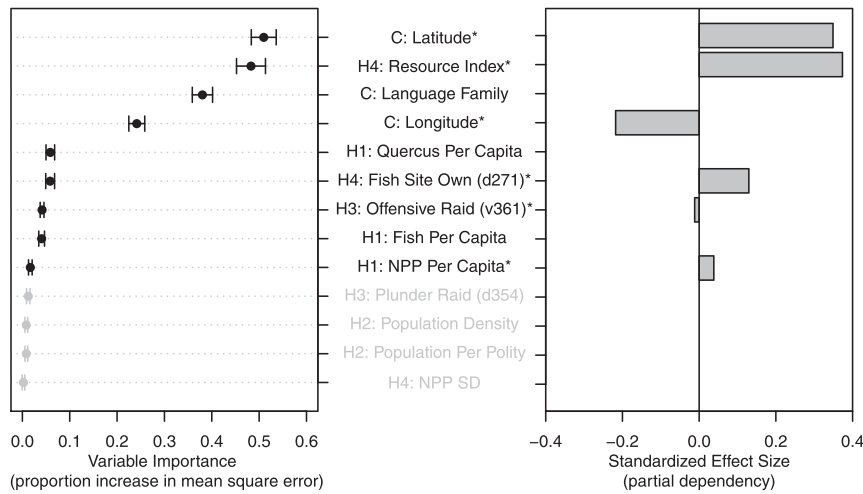
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Fig. 2. Summary of RF regression results predicting hierarchy as a function of all theoretically derived and control variables. The left panel shows the importance of each variable measured as the mean (dot) and ±2 SD (whiskers) of the proportion increase in mean square error when the variable is permuted out of the model across 50 model runs. Following automated variable selection procedures, those with the lowest variable importance (shown in gray) are dropped from the model, and only those shown with an asterisk are selected as nonredundant variables that combine to minimize prediction error, producing the best model out of all variable combinations. The right panel shows the standardized effect size for each variable included in the best model as the standardized response of the hierarchy index to change in the focal variable with all other variables held constant (partial dependency).

patches, and most but not all resource sites were either open to all polity members (i.e., communally owned) or controlled by each household.

We did not find statistically robust effects of most of the variables linked to the other three widely propounded hypotheses outlined above. Neither population pressure (indexed as per capita measures of fish harvests, acorn-bearing habitat, or terrestrial net primary productivity [NPP]) nor scalar effects of population (measured as population density or polity size) were reliably associated with political and economic inequality, although NPP per capita did have a minor association. Intergroup conflict frequency was weakly associated with hierarchy, while the importance of plunder taken on raids had a negligible effect. Nevertheless, we view these negative results as preliminary rather than definitive. Although they suggest that the variables included in H1, H2, and H3 are not necessary or sufficient for the emergence of institutionalized inequality, it is possible that they play some role in the long-term development of hierarchy, particularly in interaction with control of clumped resources, as discussed below.

In addition to facilitating differential control, resources with high spatiotemporal concentration arguably reward concentrated and coordinated labor, especially where resources offer returns to scale (52), and those who coordinate labor reap differential benefits (23). Ethnographic accounts indicate that the storable harvest from salmon streams in the Northwest Coast (hereafter NWC) region was enhanced through coordination of labor inputs by leaders (11, 12); this was especially the case farther north, where runs were of shorter duration but often higher volume per unit time (53) and more synchronized across species. This suggests that scenarios highlighting elite direction of nonkin labor (54) might account for some of our findings. Unfortunately, the WNAI database does not include variables allowing a direct test of the labor-control explanation for hierarchical leadership. However, we find it plausible that both factors—differential control of dense and clumped resource patches, plus the advantages of temporally concentrated and coordinated labor—combined to facilitate hierarchy in the form of patron–client systems, as well as slavery, in NWC societies.

In most California (hereafter CAL) societies, few resources rewarded labor coordination on a scale above the household (a

nuclear or minimally extended family) (14, 55). The managerial role for harvesting and storing key CAL resources could be and was filled by household members. Although salmon were harvested in quantity among some CAL groups, availability nearly year-round and multiple harvesting spots along lengthy river systems arguably made access control less feasible (56). Nevertheless, among the 17 CAL groups with maximum fish harvest scores (equal to those of NWC), the correlation between HI and RI was nearly as high ($r = 0.766$, $n = 17$) as for the full sample ($r = 0.881$, $n = 89$), and their mean HI (0.7) is almost twice that of other CAL groups (0.4).* Where present, CAL chiefs and their assistants played some role in redistributing resources to assist household that suffered temporary shortfalls, and in financing feasts for polity members as well as important visitors, but this was ancillary to the subsistence economy rather than being central to it (14, pp. 139–140). In contrast, NWC chiefs controlled not only resource harvesting but also distribution of the pooled resources, as well as their partial conversion into status and durable forms of wealth (5, 11, 12).

In any case, labor coordination is widely reported from many small-scale societies without being predicated on hereditary inequality; instead, leadership often rotates or goes to the currently most skilled or knowledgeable individuals (10, 57). This suggests that labor coordination or management is not sufficient to drive the emergence of institutionalized inequality, which makes it more of a consequence than a cause. Evidence presented here, as well as the broader ethnographic record, supports the conclusion that when defensible resources are sufficiently clumped and differentiated into richer versus poorer patches, some individuals or factions (e.g., kin groups) can exchange resource access for labor and other services—that is, develop patron–client systems (24, 27). In turn, this control can be reliably transmitted (in the form of hereditary property rights) to descendants (22) as was clearly the case for NWC societies.

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*Note that these simple correlations do not include linguistic or spatial controls. Both indices vary widely across these 17 cases. Interestingly, the seven cases with higher (more aquatic) RI ranging from −0.19 to 0.35 have a mean HI of 1.6, while the remaining 10 cases with RI of −0.41 to −0.71 have much lower mean HI of 0.1. The RI for the remaining CAL cases ($n = 38$) averages −0.60, and for the full sample ($n = 89$) including NWC, it averages −0.11.

Smith and Codding
Ecological variation and institutionalized inequality in hunter-gatherer societies

Table 2. Results summarizing generalized additive model selection including the degrees of freedom (df), AIC scores, and change in AIC scores relative to the best performing model

Hypothesis	Predictor Variables	df	AIC	ΔAIC
H4.1	RI* and Fishing Site Own (d271)	5.75	194.87	0.00
H4	NPP SD, RI*, and Fishing Site Own (d271)*	6.32	196.00	1.13
H4.2	RI*	5.29	196.59	1.72
Null	Controls only	4.24	199.59	4.72
H2	Offensive (v361) and Plunder (d354) Raiding	7.50	201.29	6.42
H3	Population Density and Per Polity	7.60	201.64	6.77
H1	Fish, Quercus, and NPP Per Capita	9.25	204.72	9.85

Significant terms are indicated by an asterisk (*P* < 0.05). Complete results for each model are in the supplementary materials.

Although linked to the concept of economic defensibility (46), as noted above, the patron–client model entails additional conditions (3). When key resource patches are dense and predictable, and thus defensible, but are relatively evenly dispersed across the landscape rather than clumped, theory predicts that ownership claims will tend toward equal distribution within the social group (27). At the limit, we predict little or no differentiation into resource owners and subordinates. Rather, each family group or household will maintain approximately equal access to various resource patches necessary for subsistence and cede little control over the production and distribution of these resources to others. Indeed, this is approximately what is described for most CAL societies (ref. 14, p. 130; ref. 48, p. 136). However, when key resource patches are not only defensible but also highly clumped, as is the case for NWC societies, unequal control of resource patches, and resulting inequality in wealth and power, is the expected outcome.

The finding that the RI and fishing site ownership (d271) both have a significant direct effect on hierarchy, yet the RI has only a marginal indirect effect on hierarchy mediated through fishing site ownership (Fig. 4) is surprising given the strong connection between intensive economies and private property (58). This might mean that the institution of ownership emerges more or less independently of the degree of reliance on the owned resources or alternatively that the pattern of fishing site ownership differs depending on the degree of hierarchy (as measured by our HI), perhaps due to correlated differences in the scale of ownership or patterns of property inheritance. Resolving this question, however, will take further research.

Analyses of the full set of WNAI societies (*n* = 172) have found strong associations between linguistic affiliation, spatial location, and behavioral variables (59, 60). Our focus is more restricted and hypothesis-oriented and thus not directly comparable to these efforts (but see ref. 61). Nevertheless, in our random forests analysis, RI exhibits the largest effect, with latitude having the second largest effect size (Fig. 2). Additionally, the residuals of both our final random forests (RF) model and GAM show significant linguistic autocorrelation, indicating that there is variation in hierarchy patterned by shared language family that is not accounted for in our models. Interpreting these results is not straightforward, however, as there are several reasons why linguistic phylogeny and spatial location might covary with behavioral strategies. These include habitat selection and niche conservatism, where descendent groups expand into similar environments or retain similar ecological attributes. Although a phylogenetic signal will be observed in such cases (62, 63), this is not grounds for discounting adaptive explanations for behavioral variation (64, p. 359). Classic phylogenetic methods are designed to detect independent coevolutionary events, such as convergent evolution of adaptive strategies in response to similar ecological conditions, and thus focus on evolutionary origins of traits rather than their maintenance (62). Such maintenance can logically

result from stabilizing selection as readily as from phylogenetic constraints (64).

These complexities are clearly evident in our sample. The 55 CAL groups belong to 13 different linguistic stocks and the 34 NWC groups to 9 stocks. Three patterns are noteworthy: 1) Linguistic diversity in each region is greater than in any other comparable-sized regions in Native North America. 2) There is minimal linguistic overlap between our CAL and NWC cases (a few Athapaskan-Eyak languages are found in both regions). 3) Within each region, groups speaking related languages generally occupied contiguous areas and/or similar ecologies. The extremely high intraregion linguistic diversity in pattern 1 means that any cultural features broadly characteristic of one region (e.g., hereditary elites in NWC groups) cannot be attributed to known common ancestry. The minimal overlap discussed in pattern 2 means that differences between NWC and CAL political economies will tend to conflate linguistic differences with environmental or ecological ones (e.g., salmon-dominated versus acorn-dominated economies). Within regions, pattern 3 means that neighboring groups will often be linguistically related, similarly conflating finer-grained linguistic and ecological variation.

Spatial autocorrelation raises similar interpretive issues. There is little overlap in longitude and none in latitude between the NWC and CAL cases. The HI and most of our predictor variables also show strong divergence between the two regions (*SI Appendix*, section E). Thus, spatial autocorrelation will tend to conflate proximity of groups with regional and subregional environmental and ecological variation that might not be parameterized in our models. Importantly, even when language family
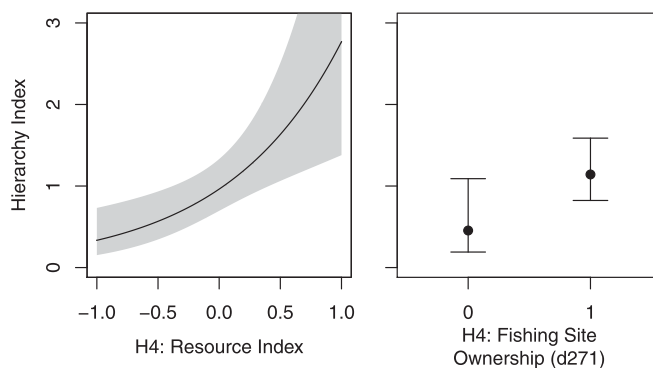

Fig. 3. Predicted partial response of the HI as a function of the RI (*Left*) and presence of fishing site ownership (*Right*) when holding all other numeric variables constant at their mean values and language family at the modal value. RI values below 0 indicate a reliance on more spatiotemporally dispersed resources (plants and terrestrial animals) over more clumped aquatic resources (primarily fish); those above 0 indicate the inverse. Shaded region (*Left*) and whiskers (*Right*) show the 95% CIs around the predicted model fit.

Smith and Codding
Ecological variation and institutionalized inequality in hunter-gatherer societies

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                        0.70
   Resource  ───────────────────────▶  Fishing Site
     Index                                 Ownership

        2.16      ╲                ╱    0.96
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                      ▼        ▼
                      Hierarchy
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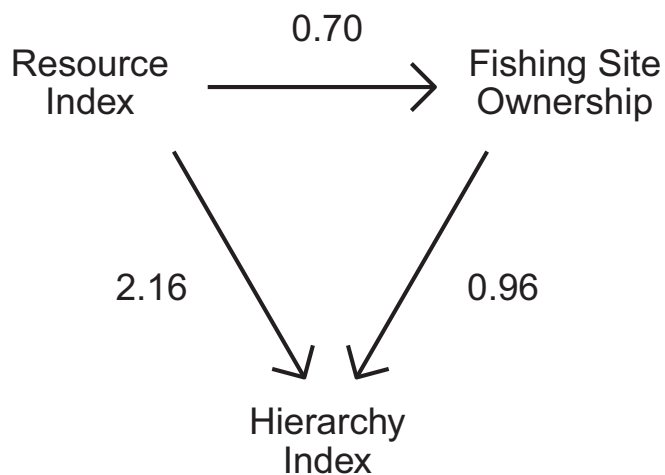
Fig. 4. Results of piecewise structural equation model showing the direct effects of the RI and fishing site ownership (FSO) on the HI, as well as the weaker indirect effect of RI on HI as mediated through FSO. Standardized coefficients (β_{std}) scaled by SD are shown adjacent to each path.

and spatial coordinates are properly controlled for, fishing site ownership and RI remain strong and the only statistically significant ($P < 0.05$) predictors of hierarchy in the GAM analysis (Table 2). Although longitude does remain an important predictor in the RF analysis, we suspect it has an effect independently from latitude primarily as a measure of distance from the coast and, given the (SE to NW) angle of the coast, is most meaningful in combination with latitude. These interpretations are evident in *SI Appendix*, Figs. S7 and S9.

One limitation of our study is the focus on ethnographic, therefore synchronic, data. Archaeological research indicates that the key features of NWC society, including elements of institutionalized hierarchy, were in place some three millennia ago and thus show considerable antiquity and stability (11). However, salmon procurement has even greater antiquity, and the shoreline environment had likely stabilized by mid-Holocene times (11). This suggests that the emergence of institutionalized inequality on the NWC was relatively gradual and may involve variables beyond those identified here. As noted above, an ancillary condition of the patron–client model is that clients' outside options are less rewarding than subordination to patrons. Factors that could reduce the value of outside options include habitat saturation due to population growth or resource depletion, growing economies of scale in resource acquisition and labor coordination, and constraints on movement due to endemic warfare, as outlined in a recent synthesis (ref. 6, p. 251). Occasional resource crises (as opposed to sustained population pressure) might force marginal communities to disband, with members seeking to join various better-favored groups, which could plausibly jump-start or enhance patron–client dynamics (31). These factors include some addressed in H1 and H3, and all potentially entail long-term dynamics involving technological change and institution building. Thus, diachronic data may be necessary to fully evaluate potential causal factors (2, 30, 31, 44, 65). However, archaeological data will always be more coarse-grained than ethnographic data, creating a trade-off between temporal depth and empirical ambiguity. Future research articulating synchronic and diachronic analyses is needed to improve our understanding of this issue.

Similarly, some of our environmental data (on NPP and *Quercus* habitat) is recent or contemporary rather than hindcasted to the 18th Century or earlier (66). We justify this on two grounds. First, our analyses only depend on relative differences

across space being stable across a few centuries (e.g., locations with high NPP values today have had that relative position over the last few hundred years). This assumption is supported by findings that modern NPP predicts historic (contact-period) population density in Native California very well (40) and is substantially correlated with density for a worldwide sample of hunter-gatherers (67). Furthermore, our *Quercus* distribution measure refers to suitable habitat for edible acorn-bearing oaks, as determined from phytogeographic data and thus a broader range than the contemporary distribution of these species. Second, hindcasting NPP and other environmental variables necessarily introduces increasing variance and uncertainties in modeled estimates and often reduces the spatial resolution of these estimates.

Unfortunately, we lack a direct measure of resource clumping or dispersion. Although we included SD of NPP (NPP-SD) as a proxy, it suffers from the fact that NPP only measures terrestrial primary production (i.e., autotrophs), excluding aquatic resources; its lack of predictive power thus is not surprising in this context. The RI captures relative reliance on aquatic (particularly salmon) versus gathered plants and terrestrial game resources. We view RI as an index of relative reliance on more clumped (fish) versus more evenly dispersed (gathered and hunted) resource patches. Although marine mammals and shellfish are included in the "aquatic resources" category, the ethnographic record is quite uniform in characterizing salmon as the largest component of the traditional diet for almost all NWC societies, and the archaeological data for the last few millennia or more is largely in agreement (68). Similarly, the evidence indicates acorns were a key staple for the majority of CAL peoples for many centuries (55, 69). However, it is clear that other taxa contributed a substantial amount to both aquatic and gathered resources.

Terrestrial game is a heterogenous category that includes large species such as artiodactyls, small game, and waterfowl. Thus, we can ask 1) are the majority of aquatic resources relatively clumped, 2) are the majority of gathered ones relatively dispersed, and 3) does terrestrial game belong in the dispersed category? For question 1, the only aquatic resources that might conceivably approach (but not equal or exceed) salmon in dietary importance are herring and eulachon, both traditionally harvested when they aggregated in brief, dense spawning runs with controlled access (70, 71). Regarding question 2, plant resources besides acorns were variably important to CAL peoples, including buckeye, mesquite, wild grass seeds, berries, and various roots and bulbs, but it appears that they rarely exceed acorns in dietary importance outside of fish-dependent northwestern California or the desert areas of southeastern California (55). In any case, few if any of these gathered resources are clumped into rich, defensible patches, so we judge the answer to question 2 is yes. As for terrestrial game, some species hunted in the study area were clumped (herd animals such as elk and pronghorn, plus migratory waterfowl), but most small game as well as deer were solitary, hence relatively dispersed. Thus, the answer to question 3 is equivocal. However, the patron–client model requires that resources be both clumped and economically defensible, and such defensibility turns on both density and spatiotemporal predictability. A salmon run is predictable in both space and (seasonally) in time, whereas clumped terrestrial resources are either mobile (artiodactyl herds) or ephemeral (migratory waterfowl), hence low in predictability. In sum, although terrestrial game in the study area cannot be classified as uniformly clumped or dispersed, we cannot think of a single important resource in this class that meets both of the requirements (defensible and clumped) for effective control by a subset of the social group ("patrons"). For that reason, we feel justified in including terrestrial game in the same category as gathered plants as a resource that cannot be monopolized.

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In sum, our analyses demonstrate that the political economies of CAL and NWC societies varied systematically in accordance with subsistence ecology—the ways in which people organized themselves to harvest resources. In turn, those contrasts in subsistence were linked to the differing characteristics of key resources, particularly their spatiotemporal distribution. Theory generates causal arguments and suggests hypotheses to evaluate those arguments, and our goal here is to do so with a set of frequently proposed explanations for variation in inequality across a relatively large sample of contiguous societies. We recognize that any synchronic analysis is necessarily limited in the inferences that can be drawn about causality. However, it is clear that the broad patterns of climate, topography, and stream physiography as they varied over the more than 4,000 km north-south range occupied by these societies largely determined the distribution of the plants and animals on which they depended. The amounts harvested and the methods used varied over time and space, but thousands of years of cultural evolution resulted in patterns of demography, labor organization, resource distribution, and property rights that were systematically adjusted to local and regional ecology. Wherever salmon occurred in sufficiently dense and localized runs, some members of a society claimed pre-eminent rights to direct their harvest and distribution. Wild plants were harvested by all the societies in our sample but only in some areas were these abundant enough to allow households to supply most of their subsistence needs and evenly distributed enough to do so without direction or control by others.

Although we cannot prove a temporal sequence with essentially synchronic data, the patterns in the data match the prediction that these resource characteristics (and associated subsistence practices) variously encouraged or discouraged the emergence of hierarchical sociopolitical systems. Alternative predictions that hierarchical systems are fostered by chronic resource scarcity (population pressure), polity size (scalar stress), or intergroup conflict (chronic raiding) do not match the data nearly as well. It will take a great deal of theoretically grounded archaeological research to establish firmer causal inferences, but several regional syntheses (6, 11, 14) generally align with our conclusions.

Our results, although restricted to a limited time and place—contact-era Indigenous societies along the Pacific coastal region from what is now California to southeast Alaska—are concordant with findings from some other regions and time periods (22, 31, 44) as well as several analytical models and simulations (21, 24, 26, 27). While further refinement and empirical work is warranted to determine how broadly the patron–client explanation for the emergence of institutionalized inequality might apply, these findings offer quantitative, cross-cultural support for the hypothesis that the ability to control dense, predictable, and highly clumped resource patches is a major factor. We expect this may prove to be broadly applicable to nonegalitarian hunter-gatherers and perhaps many other small-scale societies.

Materials and Methods

Our primary source for ethnographic data is the WNAI database (48, 49). The WNAI database contains information on 441 variables coded for 172 geographically and culturally distinct entities ("tribes") in 5 culture areas. We indicate WNAI variables as "vN" (where N is the variable number in the WNAI digital database). For certain variables, we modified the original WNAI coding to ordinal or dichotomous form, as detailed in the *SI Appendix*, section A; three WNAI variables (fish harvest, dietary percentage of gathered, and aquatic resources) were transformed from ordinal codes to point estimates. These modified variables are noted by adding the letters "o" (for ordinal), "d" (for dichotomous), and "p" (for point estimates) to the WNAI variable number.

We analyzed the 34 NWC groups and the 55 groups in the CAL culture area. Thus, we include all 89 WNAI cases in the Pacific coastal area. We exclude WNAI groups relying on domesticated crops (in the Southwest culture area) as well as the lower-density, more mobile societies in the Great Basin and

Plateau regions in the interior in order to focus on populations with comparable forms of subsistence and social scale, yet exhibiting marked diversity in political-economic inequality. The WNAI coverage of the California culture area is incomplete and in particular lacks data on several central and southern California cases with a strong marine orientation, such as Ohlone (Costanoan) and Chumash. Although the early destructive impact of Spanish missions in these areas explains this omission, archaeological and ethnohistoric research since the WNAI data were assembled provides clear evidence that Chumash polities had considerable amounts of hierarchy (5). That said, our formal analysis is not by culture area, and we make no assertions of cultural or ecological homogeneity for CAL or NWC societies.

Our analytical focus is on the degree of inequality within social groups, and thus our ideal unit of analysis is the polity, an autonomous political unit controlling a contiguous resource base but not necessarily coresiding in a single settlement (72). However, of necessity we rely on the way information is categorized in the WNAI database, which is at the level of ethnolinguistic groups ("tribes", 48). As a result, most of our 89 cases contain several polities each (mean 10, median 6; *SI Appendix*, Table S1).

Our outcome measure is a composite "Hierarchy Index" composed of the sum of dichotomous (present/absent) scores for three WNAI variables: unequal food distribution (d252), ranking within kin groups (d318), and slavery (d436). The variables included in our HI were chosen as the most appropriate WNAI measures to represent variation in institutionalized inequality relevant to small-scale societies. Their definitions, and the details of original codes and our dichotomous recoding, are provided in *SI Appendix*, section A. WNAI v252 classifies wealth distribution of "food and chattels," dichotomized for HI as either balanced (equalized) or favoring the wealthy. Since these are all kinship-based societies, d318, which codes relationships within kinship units as either egalitarian or ranked, addresses core power differentials. The third HI component, d436, indexes whether slavery is present or absent; since slaves were both a form of wealth (and often traded as such) and a means of generating wealth (through their labor), and since at least in NWC cases slave owners had complete control over the fate of slaves, including the right to sacrifice them at ceremonies, this component of HI includes inequality in both wealth and power. We view each component variable as measuring an outcome of the same latent construct (hierarchy) measured the same way (absent or present), with summing these via HI as an appropriate way to aggregate scores. To assess this, following ref. 73, we conducted a confirmatory factor analysis which indicates that HI adequately captures the latent trait (details in *SI Appendix*). Although given equal weight in HI, it is not necessary (nor do we claim) that the difference between a 0 and 1 in each measure indicates the same scalar increase in inequality. Instead, we hold that the sum of the 3 scores (i.e., the HI) should accurately represent the relative degree of inequality across the societies in the study sample.

Our predictor variables include a variety of demographic, environmental, and social data corresponding to each of the explanatory hypotheses (see below). For demographic variables, our primary sources are the two relevant volumes of the *Handbook of North American Indians* (13, 74). Several environmental variables are drawn from d-place [d-place.org (75)], and we generate additional environmental predictors using geospatial data on resource distribution (50) and environmental productivity (51). More details on the variables, sources, and coding methods are provided in the *SI Appendix*.

Given that the outcome variable contains significant linguistic and spatial dependence (*SI Appendix*, section D), we rely on two statistical approaches capable of accounting for covariance caused by shared ancestry (Galton's problem) and proximity (spatial autocorrelation). First, we evaluate the effects of all predictor variables on hierarchy in a single RF machine learning regression model (76, 77). RF builds an ensemble of decision trees to evaluate the effect of each predictor and control variable on the degree of hierarchy. RF also reliably imputes missing predictor data by weighting values according to their proximity with other cases in model iterations. The importance of each variable is determined by how poorly the model performs when the variable is permuted out of the model, measured as the proportion increase in mean square error. We rely on an automated procedure for variable selection that identifies the best subset of nonredundant variables which minimize model prediction error (78). We evaluate the standardized effect size of each variable through partial dependence by examining the scaled effect of each standardized focal variable on the response while holding all other variables constant (79). Since RF relies on "black box" prediction and cannot accommodate either combined coordinates as a single covariate or proper random effects, we also evaluate our hypotheses using more standard regression-based GAMs (80). GAMs are extensions of generalized linear models that incorporate nonlinear responses as nonparametric smoothed terms. GAMs allow us to evaluate how hierarchy responds to theoretically derived predictor variables as parametric terms,

Smith and Codding
Ecological variation and institutionalized inequality in hunter-gatherer societies

ANTHROPOLOGY

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while controlling for phylogeny and neighbor effects by including language family as a random effect and spatial coordinates as a single smoothed Gaussian process. We construct four GAMs, one for each hypothesis, using the RF-imputed data to facilitate model comparison, which requires that each model has the same cases. We evaluate model performance using term significance and model AIC scores. For each hypothesis-derived model that has significant terms, variable selection is refined by dropping the variable with the lowest standardized coefficient stepwise and then comparing each using AIC and an analysis of deviance (80). Variables selected through this procedure are then combined in a piecewise structured equation model (81) in order to assess the direct effects of exogenous (i.e., environmental) variables on the hierarchy index, as well as their indirect effects through endogenous (i.e., social) variables. Final models are checked for residual spatial and linguistic autocorrelation using global Moran's I. More detail on statistical methods and results are available in *SI Appendix*, section D.

1. K. Flannery, J. Marcus, *The Creation of Inequality: How Our Prehistoric Ancestors Set the Stage for Monarchy, Slavery, and Empire* (Harvard University Press, 2012).
2. T. A. Kohler et al., "Deep inequality: Summary and conclusions" in *Ten Thousand Years of Inequality: The Archaeology of Wealth Differences*, T. A. Kohler, M. E. Smith, Eds. (University of Arizona Press, 2018), pp. 289.
3. S. M. Mattison, E. A. Smith, M. K. Shenk, E. E. Cochrane, The evolution of inequality. *Evol. Anthropol.* **25**, 184–199 (2016).
4. C. Stringer, The origin and evolution of *Homo sapiens*. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **371**, 20150237 (2016).
5. J. E. Arnold et al., Entrenched disbelief: Complex hunter-gatherers and the case for inclusive cultural evolutionary thinking. *J. Archaeol. Method Theory* **23**, 448–499 (2016).
6. R. L. Kelly, *The Lifeways of Hunter-Gatherers: The Foraging Spectrum* (Cambridge University Press, 2013).
7. E. A. Smith et al., Wealth transmission and inequality among hunter-gatherers. *Curr. Anthropol.* **51**, 19–34 (2010).
8. M. Gurven et al., Domestication alone does not lead to inequality: Intergenerational wealth transmission among horticulturalists. *Curr. Anthropol.* **51**, 49–64 (2010).
9. C. R. von Rueden, A. V. Jaeggi, Men's status and reproductive success in 33 nonindustrial societies: Effects of subsistence, marriage system, and reproductive strategy. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 10824–10829 (2016).
10. J. E. Smith et al., Leadership in mammalian societies: Emergence, distribution, power, and payoff. *Trends Ecol. Evol.* **31**, 54–66 (2016).
11. K. M. Ames, the Northwest coast. *Evol. Anthropol.* **12**, 19–33 (2003).
12. L. Donald, *Aboriginal Slavery on the Northwest Coast of North America* (University of California Press, 1997).
13. R. F. Heizer, *Handbook of North American Indians* (Smithsonian Institution, California, 1978), vol. 8.
14. R. L. Bettinger, *Orderly Anarchy: Sociopolitical Evolution in Aboriginal California* (Univ of California Press, 2015).
15. P. Drucker, *Cultures of the North Pacific Coast* (Chandler, 1965).
16. R. G. Matson, "Intensification and the development of cultural complexity: The Northwest versus the Northeast coast" in *The Evolution of Maritime Cultures on the Northeast and Northwest Coasts of America*, R. J. Nash, Ed. (Simon Fraser University, 1983), pp. 125–148.
17. W. Suttles, "Coping with abundance: Subsistence on the Northwest coast" in *Man the Hunter*, R. B. Lee, I. DeVore, Eds. (Aldine, 1968), pp. 56–68.
18. R. F. Schalk, "The structure of an anadromous fish resource" in *For Theory Building in Archaeology*, L. R. Binford, Ed. (Academic Press, 1977), pp. 201–249.
19. B. Hayden, "Pathways to power. Principles for creating socioeconomic inequalities" in *Foundations of Social Inequality*, T. D. Price, G. M. Feinman, Eds. (Plenum Press, NY, 1995), pp. 15–86.
20. K. Ames, "The archaeology of rank" in *Handbook of Archaeological Theories*, M. D. Lanham, R. A. Bentley, H. D. G. Maschner, C. Chippendale, Eds. (Alta Mira Press, 2007), pp. 487–513.
21. A. V. Bell, B. Winterhalder, The population ecology of despotism. Concessions and migration between central and peripheral habitats. *Hum. Nat.* **25**, 121–135 (2014).
22. M. Borgerhoff Mulder et al., Intergenerational wealth transmission and the dynamics of inequality in small-scale societies. *Science* **326**, 682–688 (2009).
23. P. L. Hooper, H. S. Kaplan, J. L. Boone, A theory of leadership in human cooperative groups. *J. Theor. Biol.* **265**, 633–646 (2010).
24. P. L. Hooper, E. A. Smith, T. A. Kohler, H. Kaplan, "Ecological and social dynamics of territoriality and hierarchy formation" in *Principles of Complexity: An Introduction to Complex Adaptive Systems and Human Society*, J. Sabloff, Ed. (Princeton University Press, 2018), pp. 105–130.
25. T. A. Kohler, D. Cockburn, P. L. Hooper, R. K. Bocinsky, Z. Kobti, The coevolution of group size and leadership: An agent based public goods model for prehispanic Pueblo societies. *Adv. Complex Syst.* **15**, 1–29 (2012).
26. S. T. Powers, L. Lehmann, An evolutionary model explaining the Neolithic transition from egalitarianism to leadership and despotism. *Proc. Biol. Sci.* **281**, 20141349 (2014).
27. E. A. Smith, J.-K. Choi, "The emergence of inequality in small-scale societies: simple scenarios and agent-based simulations" in *The Model-Based Archaeology of Socionatural Systems*, T. Kohler, S. van der Leeuw, Eds. (School for Advanced Research Press, 2007), pp. 105–244.
28. L. H. Keeley, Hunter-gatherer economic complexity and "population pressure": A cross-cultural analysis. *J. Anthropol. Archaeol.* **7**, 373–411 (1988).
29. S. D. Fretwell, H. L. Lucas, On territorial behavior and other factors influencing habitat distribution in birds: I. Theoretical development. *Acta Biotheor.* **19**, 16–36 (1969).
30. D. J. Kennett, B. Winterhalder, J. Bartruff, J. M. Erlandson, "An ecological model for the emergence of institutionalized social hierarchies on California's Northern channel Islands" in *Pattern and Process in Cultural Evolution*, S. Shennan, Ed. (University of California Press, 2009), pp. 297–314.
31. A. M. Prentiss, H. S. Cail, L. M. Smith, At the Malthusian ceiling: Subsistence and inequality at bridge river, British Columbia. *J. Anthropol. Archaeol.* **33**, 34–48 (2014).
32. K. Summers, The evolutionary ecology of despotism. *Evol. Hum. Behav.* **26**, 106–135 (2005).
33. G. A. Johnson, "Organizational structure and scalar stress" in *Theory and Explanation in Archaeology*, C. Renfrew, M. Rowlands, B. A. Seagraves, Eds. (Academic Press, 1982), pp. 389–421.
34. G. Alberti, Modeling group size and scalar stress by logistic regression from an archaeological perspective. *PLoS One* **9**, e91510 (2014).
35. M. S. Bandy, Fissioning, scalar stress, and social evolution in early village societies. *Am. Anthropol.* **106**, 322–333 (2004).
36. S. Gavrilets, L. Fortunato, A solution to the collective action problem in between-group conflict with within-group inequality. *Nat. Commun.* **5**, 3526 (2014).
37. H. D. G. Maschner, The emergence of cultural complexity on the northern Northwest Coast. *Antiquity* **65**, 924–934 (1991).
38. D. Mitchell, Predatory warfare, social status, and the North Pacific slave trade. *Ethnology* **23**, 39–48 (1984).
39. J. L. Boone, "Competition, conflict, and the development of social hierarchies" in *Evolutionary Ecology and Human Behavior*, E. A. Smith, B. Winterhalder, Eds. (Aldine de Gruyter, 1992), pp. 301–337.
40. B. F. Codding, T. L. Jones, Environmental productivity predicts migration, demographic, and linguistic patterns in prehistoric California. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 14569–14573 (2013).
41. S. L. Vehrencamp, A model for the evolution of despotic versus egalitarian societies. *Anim. Behav.* **31**, 667–682 (1983).
42. R. A. Johnstone, Models of reproductive skew: A review and synthesis (invited article). *Ethology* **106**, 5–26 (2000).
43. P. Nonacs, R. Hager, The past, present and future of reproductive skew theory and experiments. *Biol. Rev. Camb. Philos. Soc.* **86**, 271–298 (2011).
44. A. Bogaard, M. Fochesato, S. Bowles, The farming-inequality nexus: New methods and evidence from western Eurasia. *Antiquity* **93**, 1129–1143 (2019).
45. K. M. Wilson, B. F. Codding, The marginal utility of inequality : A global Examination across ethnographic societies. *Hum. Nat.* **31**, 361–386 (2020).
46. J. L. Brown, The evolution of diversity in avian territorial systems. *Wilson Bull.* **76**, 160–169 (1964).
47. R. Dyson-Hudson, E. A. Smith, Human territoriality: An ecological reassessment. *Am. Anthropol.* **80**, 21–41 (1978).
48. J. G. Jorgensen, *Western Indians: Comparative Environments, Languages, and Cultures of 172 Western American Indian Tribes* (WH Freeman, San Francisco, 1980).
49. P. Gray, Western North American Indians SPSS.SAV. J. Comp. Cross-Cult. Res. 15, CD data disk (2006).
50. E. L. Little, *Atlas of United States Trees* (U.S. Dept. of Agriculture, Forest Service, 1971).
51. S. W. Running et al., A continuous satellite-derived measure of global terrestrial primary production. *Bioscience* **54**, 547–560 (2004).
52. B. F. Codding, A. K. Parker, T. L. Jones, Territorial behavior among Western North American foragers: Allee effects, within group cooperation, and between group conflict. *Quat. Int.* **518**, 31–40 (2019).
53. F. R. Schalk, "Land use and organizational complexity among foragers of northwestern North America" in *Senri Ethnological Studies*, S. Koyama, D. H. Thomas, Eds. (National Museum of Ethnology, 1981), pp. 207–249.
54. J. E. Arnold, Labor and the rise of complex hunter-gatherers. *J. Anthropol. Archaeol.* **12**, 75–119 (1993).
55. S. Tushingham, R. L. Bettinger, Why foragers choose acorns before salmon: Storage, mobility, and risk in aboriginal California. *J. Anthropol. Archaeol.* **32**, 527–537 (2013).
56. M. A. Baumhoff, "Environmental background" in *Handbook of North American Indians*, R. F. Heizer, Ed. (Smithsonian Institution, 1978), pp. 16–24.

57. Z. H. Garfield, C. von Rueden, E. H. Hagen, The evolutionary anthropology of political leadership. *Leadersh. Q.* **30**, 59–80 (2019).

58. S. Bowles, J.-K. Choi, Coevolution of farming and private property during the early Holocene. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 8830–8835 (2013).

59. S. Mathew, C. Perreault, Behavioural variation in 172 small-scale societies indicates that social learning is the main mode of human adaptation. *Proc. Biol. Sci.* **282**, 20150061 (2015).

60. M. C. Towner, M. N. Grote, J. Venti, M. Borgerhoff Mulder, Cultural macroevolution on neighbor graphs : Vertical and horizontal transmission among Western North American Indian societies. *Hum. Nat.* **23**, 283–305 (2012).

61. D. W. Sellen, D. J. Hruschka, Extracted-food resource-defense polygyny in Native Western North American societies at contact. *Curr. Anthropol.* **45**, 707–714 (2004).

62. M. Borgerhoff Mulder, Using phylogenetically based comparative methods in anthropology: More questions than answers. *Evol. Anthropol.* **10**, 99–111 (2001).

63. R. Minocher, P. Duda, A. V. Jaeggi, Explaining marriage patterns in a globally representative sample through socio-ecology and population history: A Bayesian phylogenetic analysis using a new supertree. *Evol. Hum. Behav.* **40**, 176–187 (2019).

64. T. F. Hansen, "Use and misuse of comparative methods in the study of adaptation" in *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology*, L. Z. Garamszegi, Ed. (Springer, Berlin, Heidelberg, 2014), pp. 351–379.

65. K. M. Prufer *et al*., The Classic Period Maya transition from an ideal free to an ideal despotic settlement system at the polity of Uxbenká. *J. Anthropol. Archaeol.* **45**, 53–68 (2017).

66. P. H. Kavanagh *et al*., Hindcasting global population densities reveals forces enabling the origin of agriculture. *Nat. Hum. Behav.* **2**, 478–484 (2018).

67. M. Tallavaara, J. T. Eronen, M. Luoto, Productivity, biodiversity, and pathogens influence the global hunter-gatherer population density. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 1232–1237 (2018).

68. V. L. Butler, S. K. Campbell, Resource intensification and resource depression in the Pacific Northwest of North America: A zooarchaeological review. *J. World Prehist.* **18**, 327–405 (2004).

69. M. E. Basgall, Resource intensification among hunter-gatherers: Acorn economies in prehistoric California. *Res. Econ. Anthropol.* **9**, 21–52 (1987).

70. D. Mitchell, L. Donald, Sharing resources on the North pacific coast of North America: The case of the eulachon fishery. *Anthropologica* **43**, 19–35 (2001).

71. I. McKechnie, M. L. Moss, Meta-analysis in zooarchaeology expands perspectives on indigenous fisheries of the Northwest coast of North America. *J. Archaeol. Sci. Rep.* **8**, 470–485 (2016).

72. P. Turchin, Warfare and the evolution of social complexity: A multilevel-selection approach. *Struct. Dyn.* **4**, 1–37 (2010).

73. D. McNeish, M. G. Wolf, Thinking twice about sum scores. *Behav. Res. Methods* **52**, 2287–2305 (2020).

74. W. Suttles, Ed., *Handbook of North American Indians, Vol. 7: Northwest Coast* (Smithsonian Institution, 1990).

75. K. R. Kirby *et al*., D-PLACE: A global database of cultural, linguistic and environmental diversity. *PLoS One* **11**, e0158391 (2016).

76. L. Breiman, Random forests. *Mach. Learn.* **45**, 5–32 (2001).

77. A. Liaw, M. Wiener, Classification and regression by randomForest. *R News* **2**, 18–22 (2002).

78. R. Genuer, J. M. Poggi, C. Tuleau-Malot, VSURF: An R package for variable selection using random forests. *The R Journal* **7**, 19–33 (2015).

79. G. Cafri, B. A. Bailey, Understanding variable effects from black box prediction: Quantifying effects in tree ensembles using partial dependence. *J. Data Sci.* **14**, 67–95 (2016).

80. S. N. Wood, *Generalized Additive Models: An Introduction with R* (CRC Press, ed. 2, 2017).

81. J. S. Lefcheck, piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* **7**, 573–579 (2016).

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