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Identifying key socioecological factors influencing the expression of egalitarianism and inequality among foragers

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Summary

Understanding how resource characteristics influence variability in social and material inequality among foraging populations is a prominent area of research. However, obtaining cross-comparative data from which to evaluate theoretically informed resource characteristic factors has proven difficult, particularly for investigating interactions of characteristics. Therefore, we develop an agent-based model to evaluate how five key characteristics of primary resources (predictability, heterogeneity, abundance, economy of scale, and monopolizability) structure payoffs and explore how they interact to favor both egalitarianism and inequality. Using iterated simulations from 243 unique combinations of resource characteristics analyzed with an ensemble machine-learning approach, we find the predictability and heterogeneity of key resources have the greatest influence on selection for egalitarian and nonegalitarian outcomes. These results help explain the prevalence of egalitarianism among foraging populations, as many groups likely relied on resources that were both relatively less predictable and more homogeneously distributed. The results also help explain rare forager inequality, as comparison with ethnographic and archaeological examples suggests the instances of inequality track strongly with reliance on resources that were predictable and heterogeneously distributed. Future work quantifying comparable measures of these two variables, in particular, may be able to identify additional instances of forager inequality.

Introduction

Understanding unequal resource access and patterns of behavior among foraging populations is a longstanding topic of interest (1-4), with scholars centering debate on whether the evolutionary pathway of human inequality is one of unique emergence (5-9) or suppression (10-14). Given the significant variation in inequality present among human and non-human populations (11, 15-19), it seems likely that, regardless of the evolutionary pathway, plasticity allows inequality-related behavior to respond to local environments and resource characteristics, as has indeed been extensively documented (e.g., 5, 16, 20, 21, 22). Accordingly, exploring how local conditions and resource characteristics impact the functional adaptiveness of each strategy (sensu stricto 23) will help explain under what conditions egalitarian or nonegalitarian behaviors should be favored (i.e., 5, 16, 24). While advances have been made in attempts to quantify material inequality of the past ~10,000 years, (see 25), there remains significant hurdles in making these cross-culturally comparable, applying them to more mobile foragers, and for measuring early occurrences of incipient inequality (e.g., 26). Related to this final point, studying the subtle emergence of inequality suffers from the "absence of evidence is not necessarily evidence of absence" problem.

Therefore, to better understand the individual and interactive effects of local conditions on egalitarianism and incipient inequality, here we develop an agent-based model (ABM) to explore the conditions that favor either. Building from research emphasizing the influential nature of characteristics of key subsistence resources (see below) and employing simple decisions for choosing where to settle/forage (27, 28), we use this ABM to test a) which resource characteristics have the greatest impact on favoring egalitarian vs unequal outcomes among foragers and b) how those resource characteristics interact to structure the types of ecological conditions favoring each outcome. We then link these simulation-based outcomes with ethnographic and archaeological cases and provide suggestions for future research.

Background

Here we review how key resource characteristics are hypothesized to impact the emergence of intra-group inequality through altering payoffs for human decisions, including territoriality. Territoriality and inequality are related phenomena as some form of territorial exclusion or set of property rights are a necessary but not sufficient prerequisite for inequality (i.e., 29), and many environmental and social variables proposed to influence territoriality (e.g., 1) may also influence inequality (e.g., 16). Here we follow recent work suggesting territoriality and inequality may be correlated within human populations (30) and explore key resource characteristics that scholars have hypothesized (individually or through interaction) should promote territoriality and/or inequality through payoffs for controlling access to resources. Specifically, we investigate resource predictability (1, 16), abundance (1, 31), heterogeneity (5, 15, 32, 33), the economy of scale or *Allee effect*

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of resources (32, 34-36), and the monopolizability (or ability to control access) of resources patches (5, 35, 37-39) which we summarize below.

The importance of predictability of resources for territoriality and inequality strongly derives from the economic defensibility model (1). If resources are predictable, individuals know where and when they can be defended which may: a) reduce mobility, enabling greater time for defense over movement (a mobility-defense tradeoff) and, b) enable individuals to have confidence in payoffs for investing in exclusionary and controlling behaviors. Increased predictability, in a patron-client framework (more detail in Supplement 1), also allows would-be patrons to consistently predict the availability of resources at their disposal to offer in exchange for client subordination (1, 5, 16).

Abundance, the second key characteristic from Dyson-Hudson and Smith (1), may vary the payoffs to controlling access. When treated as the total amount of the primary resource within the overall landscape, increasing abundance beyond the minimum required for survival could reduce the amount of space individuals need to claim, and defend (1, 37), potentially favouring an unequal distribution of resources. However, if key resources are highly abundant and/or present in super-abundances it may make resource defence and control less profitable than other options, particularly if they are homogeneously distributed on the landscape (see below). This then suggests that intermediate abundances, those above the minimum needed for survival but below high or super abundances, may promote inequality. Within this gradient, lower intermediate levels of abundance may produce greater likelihood for inequality than higher abundances. Given these divergent impacts, several studies question the uniform application of the economic defensibility model (40, 41), and suggest additional environmental and resource characteristics are necessary for understanding territoriality and inequality.

Spatial distribution of the primary resource within an environment is one of the characteristics that has received increasing attention (e.g. 5, 15, 32, 33, 35). Highly heterogeneous environments, those where resources occur in some restricted locations but not in others, may have cascading consequences for both territoriality and inequality. Such environments may favour denying access through either preventing too much diminution of returns (32) or enabling holders to make use of resources to obtain concessions from others through exploitation or leadership (15, 31, 42). Further, increasing heterogeneity, much like predictability and abundance, can decrease mobility, potentially making more time available for exclusionary and/or controlling practices. Finally, heterogeneity may circumscribe resource acquisition opportunities by severely limiting alternate options and thereby favouring nonegalitarian outcomes (i.e., environmental circumscription 15, 43).

Scholars have also nominated the economy of scale, or Allee effect (34, 35, 44), as a resource characteristic impacting exclusionary behaviors. Foundational work (45) demonstrated that fitness benefits can emerge through increasing the number of cohabitants in an area, although this benefit is not linear and reaches tipping points where adding more cohabitants reduces the benefit to each individual. Through these dynamics, Allee effects can have significant consequences on behavior (46, 47) including promoting cooperation. Resources with larger economies of scale could decrease the cost of defense for each individual if defense costs are partly shared or coordinated. In such cases, individuals may be incentivized to cooperate for defense, presenting opportunities for leader or patron based intragroup inequality whilst favoring territoriality (31, 48-50).

Finally, a resource's monopolizability, or the relative ease with which an individual or faction may control use of a resource patch (16, 35, 37), should influence emergence of egalitarian or unequal behaviors. Monopolizability may be conceptualized as a composite characteristic driven by the interaction of factors such as a) the need for costly extraction and/or production technology (35, 51), b) how readily stored the resource is (39, 52, 53), c) the amount of space required to be defended within a patch (37), d) the opportunity cost imposed by defending / excluding others from the resource (1), and e) the value of a unit of the resource to a person who has it and someone who does not (38), all of which may also contribute to the degree to which the resource may be considered a private versus a public good (9, 42). These characteristics are hypothesized to then interact with a resource's predictability, abundance, heterogeneity, and economy of scale to further influence if individuals will pay the cost to exclude/control or not. Monopolizability may be thought of as a *within-patch characteristic*, while the predictability, abundance, and heterogeneity of a resource are *landscape-level characteristics* of resource distributions. For example, reliance on small seeds (i.e., 53) represents the use of a primary subsistence resource requiring relatively immobile processing tools (e.g., metates) and that is easily stored (37). This may result in a lower relative cost (and higher incentive) for monopolizing compared to, for instance, large game mammals, even if the seeds and game had equal predictability, abundance, heterogeneity, and economy of scale.

Resource characteristic influences on inequality are also impacted by changes in human population density as changing density may alter landscape carrying capacity, increase or decrease competition for resources (42, 54), and/or alter circumscription. All of these may structure viable alternate options for acquiring resources (5, 15, 55) such that egalitarian/unequal or territorial/non-territorial strategies may pay off better. However, research suggests that population size and/or density change alone is not a sufficient explanatory cause and must be paired with other factors (5, 56), such as the characteristics of resources above.

In summation, each of these key resource characteristics are predicted to influence egalitarian versus nonegalitarian outcomes among humans. Further, these characteristics are expected to have interactive effects, as demonstrated by Smith and Codding (16) and Boone (42), among others.

Predictions

Based on the above literature, we make two general predictions:

- **P1**: Egalitarian outcomes will be favored in environments where resources are a) not predictable, b) highly abundant, c) homogeneously distributed, d) have a small economy of scale, and e) when resource patches are not easily monopolizable.
- **P2**: Unequal outcomes will be favored in environments where resources are a) predictable, b) less abundant, c) heterogeneously distributed, d) have large economies of scale, and e) when resource patches are more easily monopolizable.

Methods

Agent Based Model

To evaluate these predictions, and our broader questions, we implement an agent-based (individual-based) modeling (ABM) approach here. ABMs are explicitly designed to enable the evaluation of systems that may be hard to observe in the "real-world" and to explore behavioral interactions across multiple scales, allowing for complex pattern emergence from simple behavioral decisions (57-60). The purpose of our model is to evaluate the relative influence of key subsistence resource characteristics on the emergence of a dominant behavioral outcome: egalitarian or nonegalitarian. Specifically, we address the following two questions: when individuals pursue the best options for themselves, a) which resource characteristic most strongly predicts egalitarian and nonegalitarian outcomes, and b) which combinations of characteristics most favor each outcome. A detailed model description, including full agent behaviors and the theory underlying them, following the ODD (Overview, Design concepts, Details) protocol (61), is provided as Supplement 1 with the complete model code, written in NetLogo (62), available as Supplement 2. Below we provide an adapted version of the ODD. The model here shares some similarities with several prior models (8, 30) to explicitly advance understanding of the influence of subsistence resource characteristics on incipient inequality.

Entities

The model includes the following *entities*: agents representing individual foragers who seek to maximize their rates of gain and square grid cells representing foraging patches with extractable resources. At initialization, 876 agents are created and tracked through the model run. The full set of state *variables* characterizing these entities are available in Supplement 1. Rate of gain is characterized by suitability, following Greene and Stamps (28) eq. 1. A single model step represents the amount of time required to extract resources from a patch. This is deliberately abstract so that different model setups may represent different resource types. Time occurs both within and between a single model time step, with two individual turns occurring per time step (see *Behaviors* below for more detail). Model simulations are run on a gridded landscape of 10 x 10 cells, each representing a patch of land with resources capable of supporting multiple individual agents.

Processes

The most important *processes* for agents within the model, repeated every turn (twice per tick), are the identification of the optimal patch, movement, evaluation of defense, and recording of returns. At the end of every tick, agents also undertake evaluation of whether to change strategy or not. On the first turn of each tick, each agent's first action is to evaluate the landscape for the patch that will provide them the highest rate of gain. Agents' patch choice is restricted to patches that either are already occupied by agents employing the same strategy as the agent or patches without an established strategy for the turn. This emulates per turn positive assortment (see 63, 64, 65). The second action each agent takes is to attempt to move to the best available patch.

Agents employing an egalitarian/nonterritorial strategy or moving to patches not yet claimed on the turn are always able to join this best patch. When an agent attempts to join a patch currently occupied by unequal agents, these current occupants evaluate if they will defend the patch or not. This evaluation is the third action an agent may take on each turn. If current occupants defend a patch it is removed from the options for all subsequent agents as well as the agent currently attempting to move. This moving agent, unable to join their preferred patch, undertakes the fourth potential action of their turn, identifying and attempting to move to the second-best patch. The evaluation of defense of a patch and finding the next best patch repeats until the agent has a location to occupy. Once all agents have moved for the turn, they record the suitability of the patch they are occupying (i.e., their returns) minus any costs they paid for defense and/or supporting a leader or plus any benefit they gained as a leader. After this, if resources are not completely predictable, at least some will move about the landscape (see Supplements 1 & 2).

Then begins the second turn of the tick. Agents with territorial/unequal strategies defend the same location, not moving, and therefore skip all actions apart from recording returns gained (see *Behaviors* for more information). Egalitarian agents, however, repeat actions one, two, and five. Once all agents have performed both turns on the tick, they compare their resource gains for the overall tick with a random agent on the landscape, the fifth action. If the comparison agent obtained greater returns than the ego agent, the ego agent changes their strategy to that of the comparison, otherwise the ego agent keeps their current strategy for the next tick. Use of a random agent comparison emulates adaptative shifts of strategy through observation and is implemented to avoid deterministic forcing of agents to a single strategy. As individuals optimizing are likely to target the best return they can find, not the mean that improves the return for everyone, we allow agents to alter their strategy to emulate emergence of a preferred strategy resulting in egalitarian or nonegalitarian outcomes that reacts to resource characteristics and the decisions of other agents. For a step-by-step breakdown of the model progression, please see Supplement 1.

Resource Characteristic Parameters

To evaluate the influence of various environments, the model landscape is parameterizable with many unique combinations of resource characteristics. Each of the five resource characteristics may be set to one of three levels, representing low, middle, and high values for the parameter. To maintain focus on the influence of resource characteristics, human population size is held constant. The assigned levels (low, middle, and high) for each resource characteristic variable are based on ethnographic observations (see below) and enable us to parameterize the model within a reasonable model space, allowing for different model setups to represent reliance on different types of key subsistence resources.

To establish low, middle, and high values for abundance, heterogeneity, and economy of scale (Allee effect), we employ the 25^{th}, 50^{th}, and 75^{th} quantile values from ethnographic proxies (Table 1; Supplements 1 and 3). Proxies are derived using all foraging and fishing societies in the Binford Hunter-Gatherer data set (66) via the **Binford** package (67) in the R statistical environment (68) and from a recent addition of environmental data to the Standard Cross-Cultural Sample (SCCS) (15). Proxy values for abundance and heterogeneity are taken from the mean and standard deviation (50km) in net primary productivity (NPP) from the MODIS satellite imagery (69, 70) following Wilson and Codding (15) for each unique society. The proxies for economy of scale and population size (Table 1) come from Binford variable Group 1, the size of the smallest group that regularly cooperates for subsistence, and from the population of ethnic group estimates in the Binford dataset (B006 from 71). Human population size is held constant at the 50^{th} quantile value for all model runs. We use Binford Group 1 estimates for a rough economy of scale proxy as there is a lack of broad cross-cultural estimates of economy of scale, and to strike a balance between the economy of scale and the smallest group sizes at which material differences may emerge. However, this measure likely over-estimates economy of scale as it will include individuals who may not be involved in primary production, and it may not capture the ideal scales at which we should expect to see material differences emerge. Given these limitations, we conduct a sensitivity analysis on the economy of scale, varying optimal group sizes from 1 to 100 while holding all other resource characteristics constant at their least, middle, and most theoretically likely to promote inequality values (see Supplement 3 for more detail).

Predictability and monopolizability lack comparable cross-cultural ethnographic estimates from which to establish parameter spaces in the same manner, and, therefore, low, middle, and high values are established a priori (Table 1). For predictability, we build landscapes where a) resources redistribute on the landscape every turn (not predictable), b) 50% of patches have resources redistribute every turn (somewhat predictable), or c) resources are never redistributed (completely predictable). To deal with the reality that monopolizability is a composite outcome of multiple features, we implement a cost value, modeled as the suitability lost (e.g., opportunity cost, time/risk expenditure, or defensive investment) if a single agent alone defended the average patch (See Supplement 1 for full details). This value may be thought of as the foraging time, energy, and/or other resources lost resulting from the composite investment an agent puts into non-foraging activities that enable monopolization to occur. Higher or lower values of this defense cost then represent situations where monopolization may be easier or more difficult (i.e., more or less time, energy, and resources spent in non-foraging activities to enable monopolization), based upon the components of monopolizability such as storability, within patch space needed to be defended, reliance upon expensive technology, etc. Unfortunately, cross-cultural ethnographic estimates of the cost expended to claim exclusive access to resources are rare or non-existent. Thus, to better try and understand its influence and identify reasonable cost values we use a broad sensitivity analysis (72) and pattern-oriented modeling approaches (73) (see Supplements 1: Lines 149-190 and 3: Lines 147-180 for more details).

Behaviors

The key *design* concepts in this model relate most directly to implementing resource access strategies. Behavioral strategies in the model follow the theoretical descriptions in Supplement 1. All agents are rate maximizers with perfect landscape knowledge following underlying assumptions from simple settlement decision strategies (27, 28). Egalitarian agents never exclude others, meaning they move to the best patch available to them and each agent receives the patch suitability at the end of the tick as their returns. As each time step in the model is split into two potential movement periods (turns), we follow economic defensibility theory (1) and allow agents who practice the free access strategy to favor mobility in a mobility-defense tradeoff. Therefore, free access agents may move during each turn of a tick, a unique aspect of this strategy.

Unequal resource access agents make the opposite tradeoff, favoring the ability to exclude over the ability to move; in other words, experiencing a mobility-defense opportunity cost. Following first-mover principles, the first such agent to claim an available patch becomes the leader/patron for that turn. Any subsequent agents joining that patch pay a cost (i.e., 28 equation 2) which is removed from their returns and given to the leader/patron. Joining agents know the cost and evaluate payoffs versus returns from joining a different patch. This emulates the functional outcome of either managerial mutualism (8, 31, 48, 49, 74) or patron-client (15, 36, 42, 43) forms of inequality whereby individuals give up resources or autonomy to an individual who enhances their performance (i.e., a leader) or to a patron in return for access. As both managerial mutualism and patron-client strategies may produce similar outcomes, occur at the same time, or lead to one another, as recent work suggests (75), we do not evaluate the two pathways separately, focusing instead on egalitarian vs nonegalitarian outcomes overall. However, future iterations could allow this to emerge or to be negotiated to explore additional questions. We do run a broad sensitivity analysis on joining cost by varying the cost up and down, while holding all other resource characteristic values at their least, mid, and most likely to promote inequality levels, to evaluate how altering the parameter influences outcomes (Supplement 3).

Per the mobility-defense tradeoff, agents engaging in an unequal access strategy only move on the first of the intraturn movement periods. These agents exclude others from the patch they settle only once the leader/patron deems such exclusion to be in their best interest (see Supplement 1 for equations and calculations). These agents will then defend the location for the second of the intraturn movement periods. The cost of excluding others is split equally among all agents on the patch, representing the loss suffered by each agent resulting from exclusionary actions either due to direct participation in defense or to the decrease in returns experienced as a result of some individuals spending time on defense that otherwise would have enhanced the Allee effect.

Model Simulation

To evaluate the influence of individual, and combinations of, characteristics, we use 243 unique combinations of the five key resource characteristics. Models are run until 200 ticks (400 turns) have elapsed. We use 200 ticks as a cutoff to balance identification of characteristics that strongly favor each strategy and computational intensity. As stochasticity is built into the model setup, order of agent movement, agent comparison of resources, and redistribution of resources when landscapes are not completely predictable, we run 100 iterations of each parameter combination, producing 24,300 distinct model runs. Key model outputs from each run are the levels of each resource characteristic (i.e., low, middle, or high) and the proportion of agents employing each strategy across the model run. To calculate this, within each run, on each tick (n = 200), we record the proportion of agents employing the egalitarian and nonegalitarian strategies. At the end of the run, we export the mean of the 200 observations, providing the proportion of agents employing each strategy across that run for each of the 24,300 runs. This average proportion allows us to assess whether the model favors egalitarian, nonegalitarian, or mixed outcomes.

Future Extensions

The model created and analyzed here is, of necessity, a generalization of the world based upon simplified agent decisions; yet predicting egalitarian versus nonegalitarian outcomes is necessarily complex. Our intent is for this baseline model to be alterable by future scholars for incorporation of additional variables likely to influence egalitarian and nonegalitarian outcomes such as: variation in resource holding potential (24), directly measuring circumscription (42, 43, 55), free-riding and collective action with potential solutions (76, 77), leader/patron and follower/subordinate optimization (36), kin selection, social levelling mechanisms, allowing agents to claim more than one grid cell, separate male-female foraging goals (37), cooperative levelling (4), breakdowns of the defense cost into multiple subcomponents, varying human population sizes, or implementation of the current behaviors in a model world built on real-world local environments with directly observed ethnographic behavior for pattern matching. The model may also be linked to other extant models such as ABM implementations of Sahlin's model exchange of exchange (78) for investigating scarcity influences (e.g., 79) or investigations of polity and formation and territoriality (30, 80). Additional extensions may productively further explore assumptions within the current model setup, such as rate maximization, perfect knowledge, and positive assortment.

Statistical Analyses

Given we investigate 243 parameter combinations run 100 times each, we employ random forest (RF) (81, 82) machine learning regression implemented in the R statistical environment (68) to evaluate how variation in each resource characteristic influences egalitarian or nonegalitarian outcomes. RF is an ensemble decision tree approach evaluating how the dependent variable is influenced by each predictor, even if highly correlated (81). Here the predictor variables are the five resource characteristics described above. The dependent variable is the proportion of agents employing the unequal strategy, which can be thought of as probability of inequality The RF model is evaluated using root mean square error (rmse) of prediction and variance explained from tenfold cross-validation using the **spm** package (83) as well as by checking model residuals for normalcy. To identify which resource characteristics have the greatest impact we employ variable importance, which is determined by permuting variables out of the model and measuring the increase in mean square error (mse) as a result (82).

To further evaluate predictions, we generate the standardized effect size through partial dependence response of the dependent to each independent variable while the others are held constant (84). To better understand the interactions between the other resource characteristics and monopolizability, we generate 12 distinct partial dependence response estimations providing three sets of partial dependence responses per level of monopolizability. For each characteristic's evaluation, the other four predictor variables are held constant at their levels least, middle, and most theoretically likely to promote unequal outcomes. All simulation output data for this analysis is available in Supplement 4 and the sensitivity and analytical code to replicate this work is available in Supplement 3.

Results

Depending on the model setup, the proportion of egalitarian to nonegalitarian individuals varies greatly (Supplement 3), though the distribution is strongly bimodal (Figure 1). The RF model performs well in predicting the proportion of nonegalitarian individuals across each model run (cross-validated variance explained = 86.95%, rmse = 0.14), with model residuals normally distributed around zero (Supplement 3).

Variable importance, measured as the increase in mean square error (MSE) and the increase in node purity resulting from permuting the variable about of the model, suggests each predictor variable has an important impact on the proportion of agents ending a run in a nonegalitarian outcome. Monopolizability, though, has by far the largest individual influence (Figure 2).

As defense cost parameterizing monopolizability has greater influence than the other predictor variables, we initially evaluate its partial response separately (Figure 3). When unequal access is least theoretically likely based on the other resource characteristics (i.e., high abundance, low heterogeneity, low economy of scale, no predictability), but a resource patch is easily monopolizable, we find greater than 50% of individuals employ an unequal access strategy, or a greater than 50:50 probability of inequality. If a resource patch is more costly to monopolize though, the proportion employing a nonegalitarian strategy falls to near zero. When all other resource characteristics are held at their mid-values the pattern is the same; a low monopolizability cost leads to unequal outcomes whereas increasing costs leads to more egalitarianism. When all other variables are most theoretically likely to promote unequal access (i.e., high heterogeneity, low abundance, high economy of scale, and complete predictability), we find that inequality is likely at any of the simulated levels of monopolizability.

Partial responses for heterogeneity, predictability, abundance, and economy of scale show their interactions with each other and with monopolizability do influence unequal or egalitarian outcomes (Figure 4). When monopolizability is held at its mid-value and all other variables are held respectively at their values least, mid, and most likely to promote unequal access, most variables have a relatively similar impact on the proportion of agents ending with inequality. Increases in heterogeneity, predictability, and economy of scale increase the probability of inequality. Increasing abundance decreases it, though the effect is relatively muted.

The overall pattern in the interactions is the same when the monopolizability cost is held at its high point (hard to monopolize) and all other variables are held respectively at their values least, mid, and most likely to promote unequal access. Increasing heterogeneity, predictability, and economy of scale increases the probability of inequality while increasing abundance decreases it. However, unlike the interactions when the monopolizability is held at its midpoint, the variables' influences are not as evenly distributed. Heterogeneity is much more influential than the others when it is costly to monopolize, followed by predictability (Figure 4). Economy of scale and abundance have less impact.

Inequality is always more likely than random chance (>50%) regardless of variation in resource characteristics when the monopolizability cost is held at its low point (easy to defend/monopolize). Further, when it is not very costly to monopolize, heterogeneity and the economy of scale have small impacts. Decreasing predictability does decrease the proportion of agents employing the unequal strategy, and, when all other characteristics are held at their least likely to promote inequality value, so too does abundance. However, neither characteristic drops the inequality probability below 50%. As the interactions are many and complex, Table 2 provides a qualitative assessment of the interactive impact of resource characteristics on strategy outcomes.

Broad sensitivity analyses suggest varying the leader/patron cost, monopolizability, or economy of scale do not qualitatively change results (see Supplement 3, Sensitivity Analyses). When holding all other variables constant at their least likely to promote inequality values, changing the joiner/kickback cost has no impact on the probability of inequality – even very minimal costs for leader/patrons cannot outperform egalitarianism (Supplement 3 Figure 2a), When all other variables are held at their middle values, decreasing the joiner/kickback cost increases the probability that the run will result in unequal outcomes as agents receive the benefit of a leader while paying little cost, whereas increasing the cost (i.e., making leaders/patrons more costly/exploitative) decreases the probability of an unequal outcome (Supplement 3 Figure 2b). When all other variables are likely to promote inequality, even expensive leader/patron costs result in inequality (Supplement 3 Figure 2c). Varying the costliness of monopolizing a resource patch, when holding all other variables constant at their least and middle values, produces a sigmoidal distribution where there is a high probability of nonegalitarian outcomes when it is cheap to monopolize and a low probability when the costs increase (Supplement 3 Figure 3a,b). When all other variables are held at their most likely to produce inequality, even high monopolizability costs produce inequality (Supplement 3 Figure 3c). Given the generally sigmoidal relationship, we evaluated the influence of the defense cost at a relatively low, mid, and high value to capture how it interacted with other variables. Varying the optimal group size (economy of scale) beyond the values in the main analyses above does not change outcomes. Small group sizes favor egalitarianism and larger aggregations favor inequality, although the strength of the relationship varies dependent upon the values of the other resource characteristics (Supplement 3 Figure 4).

Discussion

Overall, the results support predictions 1 and 2. In general, individuals are more likely to maintain egalitarian strategies most frequently when resources are not predictable, highly abundant, homogeneously distributed, and have a small economy of scale, regardless of defense cost value (P1). Conversely, an unequal access outcome is most likely when resources are completely predictable, less abundant, heterogeneously distributed, and have a large economy of scale (P2). However, the strengths of these relationships vary based upon the interactions of the characteristics (Figure 4), particularly in how the landscape distribution characteristics (predictability, abundance, and heterogeneity) interact with the patch characteristic (monopolizability).

When a resource is easily monopolized, payoffs for excluding and/or controlling are relatively unaffected by any other characteristics (Figure 4:i-l). Relying on key subsistence resources that are greatly benefited by storage, significant technological investment, etc., favors greater than a 50% chance of nonegalitarian outcomes even if the resource is highly abundant, has little heterogeneity in its distribution, has a small economy of scale, and is not very predictable. The probability of nonegalitarian outcomes only increases as these characteristics increase in their theoretical likelihood to promote inequality.

Ethnographically, the Pacific Northwest of North America may present a case study of this relationship where reliance on anadromous fish produced steep levels of inequality (16, 85). These fish (fish runs) may be expected to be easier to control (or monopolize), and to provide incentives to do so, based on how readily they are stored, the expensive technology used for exploitation (86), and the decreased space required to be defended (16). Indeed, Smith and Codding (16) show that groups in the area dominantly reliant on anadromous fish experienced significantly higher levels of inequality than groups more reliant on plant resources requiring greater mobility. There is also evidence of interactions with the other resource characteristics as, in more northerly locations where the fish runs were more heterogeneously distributed and predictable, inequality was even more prevalent. Similarly, recent work exploring leadership and inequality among the arctic Iñupiaq of Northwest Alaska argues for a patron-client style relationship among whaling boat captains (*umialik*) and boat crews (87). The Iñupiaq subsistence system relies heavily upon storage and implements expensive technology (e.g., whaling boats), which may incentivize monopolization. While the scope of inequality is different between these two cases (considerably lower and more transitory among the Iñupiaq), this may be evidence of the interaction with the other resource characteristics as whales are likely less predictable and heterogeneously distributed than the salmon runs. Still, both cases appear to be instances where the monopolizability of a key resource may take a leading role in experienced inequality.

The relationships and interactions between resource characteristics get more complicated when resources are less easily claimed (Figure 4:a-h), however. Even when egalitarian outcomes may be expected due to a high monopolization cost, landscape level resource characteristics can push the probability of inequality well above 50%. This suggests that, to explore if individuals are/were likely to experience egalitarian or nonegalitarian relations, while it may be important to estimate the relative monopolizability of the key subsistence resources, it is also necessary to understand and measure the landscape distribution characteristics.

Consistently, when monopolizability is more costly, we find that increasing heterogeneity in the distribution of resources increases the probability of inequality. This fits theoretical expectations as when resources are concentrated into a few, limited, areas the payoffs for monopolization increase either from more resources able to be held by a single defensive action and/or heterogeneity structuring payoffs such that guaranteeing access to some resources, even if as a subordinate, is better than remaining egalitarian in a much poorer location. The influence of heterogeneity was shown recently in a global cross-cultural study which found that increasing heterogeneity in local environments significantly increased the probability that ethnographically documented societies possess inequality, with the relationship particularly strong in foraging and fishing societies (15: Figure 4), suggesting that individuals within such populations may be especially influenced by the heterogeneity in the distribution of their key subsistence resource(s).

In a specific ethnographic context, it has been suggested that there is significantly greater intragroup inequality between individuals within Papua New Guinea groups who are fisher-foragers than those who are hunter-foragers, despite neither set of groups relying much on storage (88, 89). Crucially, the hunter-foragers rely on resources relatively homogeneously distributed, though unpredictable, whereas fisher-foragers rely primarily on resources that are highly concentrated in limited areas (heterogeneous) and highly predictable in their distributions (88). These resource characteristics then structure divergent payoffs for different political actions geared toward obtaining power and inequality (89). Archaeologically, heterogeneity appears to play a role in the early stages of hierarchy and inequality among the forager-hunter-gatherer Calusa of modern-day Florida. While the key marine resources comprising large portions of the diet may or may not have been very predictable over several generations, they were relatively predictable on shorter timescales and, importantly, heterogeneously distributed, a factor that has been associated with the emergence of more complex Calusa patterns and incipient hierarchy in the area (90).

Like heterogeneity, predictability produces a consistent pattern when the monopolizability costs are higher, with increasing predictability increasing the probability of inequality. Ethnographically, examples of this influence exist from Indigenous foraging populations in both Papua New Guinea (see above) and populations who lived (and continue living) in modern day California. Among these Californian groups, Bettinger observes that, "*The key difference was that the easterners became reliant on pinyon, which was unpredictable, leading to the development of nonterritorial family bands. The westerners, on the other hand, became reliant on the acorn, which was dependable enough to justify landholding and territorial defense from the outset, leading initially to patrilineal bands*" (91: 176-177). Increasing predictability may, in part, also relate to incipient inequality or social differentiation among the early Natufian complex foragers, where rising temperatures and precipitation appear to have improved the predictability of key resources, increasing the reliability with which these foragers could locate and exploit them (92-94).

Unlike both heterogeneity and predictability, abundance appears to be less important as the cost to monopolize increases, evidenced by the minimal change in the probability of inequality across the majority of interactions for mid and high monopolizability costs (Figure 4). This is perhaps unsurprising. So long as key resources are abundant enough to both enable survival and to provide subsistence support for additional individual(s) beyond the person(s) currently using the resource (ie., surplus, c.f., 5, 7, 95), any relative overall abundance increase or decrease may not alter the options available to individuals drastically unless a resource experiences a spatiotemporally limited "super abundance" (1), something likely unique to limited circumstances.

Finally, resource economy of scale is relatively unimportant if the other characteristics are all at their low or high values (Figure 4). However, when the key resource is moderately heterogeneous, predictable, and abundant, the economy of scale may have a large impact through its promotion of human aggregation. Though this may sound like a restricted combination of characteristics, it is likely that many resources are somewhat predictable, somewhat abundant, and moderately heterogeneously distributed, suggesting the economy of scale may have a larger impact than previously identified. From a managerial mutualism perspective, ethnographic evidence of this effect exists in the Great Basin of North America. Here group cooperation favored by large returns to scale from cooperating for antelope and rabbit drives produced situations in which many individuals aggregated together under a temporary leader, deferring to these individuals for the purpose of acquiring these key resources (96: 34-36, 61). While this is a different kind of inequality (transitory) and certainly less severe in scope compared to foragers in the Pacific Northwest and several other areas, these instances of aggregation based on the economy of scale of the resources incentivized and relied upon intragroup differentiation (leader and followers).

Here we have matched ethnographic and archaeological examples of foraging populations with inequality as opposed to the more common circumstances of relative egalitarianism among foragers. We did this to emphasize how local conditions may favor the rarer behavior; however, our model does provide an explanation for the prevalence of enduring relative material egalitarianism among many foraging populations as well. We suspect most foraging populations rely on resources that are/were some combination of relatively unpredictable, homogeneously distributed, more abundant, and with smaller economies of scale. Long-term reliance on such resources should favor egalitarian outcomes by reducing the payoff for exclusionary or controlling behaviors. That said, we welcome research identifying instances where this is not the case and inequality remains absent as these cases will likely provide key insight into other mechanisms limiting inequality. Finally, the patterns in the emergence of material inequality documented here may represent similar decision processes as those suggested to later lead to increasing intergroup hierarchy and polity formation, particularly among agricultural populations (80), presenting an intriguing potential direction for future research as agriculture may often be described as quite heterogeneously distributed and highly predictable. All our results will benefit from further ethnographic and archaeological testing, some of which is seen in the other articles in this special issue.

Conclusion

Overall, our work here employing an ABM connecting several theoretically informed hypotheses provides three key findings: **a)** The monopolizability of a resource, a factor difficult to empirically quantify, has a significant, but contingent, impact on whether individuals may engage in more egalitarian or nonegalitarian relations based upon other landscape level resource characteristics. **b)** When it is even somewhat costly to monopolize/control primary resource patches, landscape level resource predictability and heterogeneity in distribution, in particular, will structure the type of behavior that pays off the most. This suggests that estimating these aspects of primary subsistence resources across the spatial and temporal diversity of human groups will be particularly fruitful in understanding incipient inequality. And **c)** as behaviors that suppress or engage in hierarchical interactions are both in the human behavioral toolkit (i.e., 97), it is the local ecological conditions structuring payoffs to individuals that should promote either egalitarian or nonegalitarian behavioral outcomes. While certainly interactions with other factors like private property (9, 98), relatedness with others (c.f., 43), intergenerational wealth transfer (17), and demographic changes altering labor monopolization (95, 99) also played a role and warrant examination in the expression of past inequality, future work measuring and estimating the heterogeneity, predictability, and economy of scale of key subsistence resources, in particular, will prove highly productive in predicting egalitarianism and non-egalitarianism emergence in the past.

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Tables

Variable	Proxy	Low Value	Mid Value	High Value	Source
Abundance	Net primary productivity (NPP) (50km radius)	~1700	~3300	~5700	(15, 66)
Heterogeneity	Standard deviation NPP (50km radius)	~700	~1400	~2600	(15, 66)
Economy of Scale	Smallest cooperating group size	11	16	20	(66)
Population Size	Total population	386	876	2000	(66)
Predictability	% Patches keeping same productivity each turn	0%	50%	100%	--
Monopolizability	Amount suitability lost for a single agent to defend the mean patch	3	7	11	--

Table 1. Global environment state variables. Values for most resource characteristics were obtained from ethnographic proxy observations. Low, mid, and high values for abundance and heterogeneity are derived from the 25th, 50th, and 75th percentile NPP values for foraging societies within the Binford and SCCS datasets. The economy of scale and population size values are the 25th, 50th, and 75th percentile values from foraging societies within the Binford dataset. Predictability and monopolizability are set a priori from theoretical expectations (see main text and Supplements 1 and 3).

Monopolizability Cost	Other Characteristic Levels	Inequality Outcome
Low	Least	Inequality is likely, but even more probable when there is complete predictability and low abundance
	Mid	Inequality always likely, but least probable when resources are not predictable and highly abundant
	Most	Inequality always likely, but least probable when there is no predictability
Mid	Least	Inequality is uncommon, but most probable when there is high heterogeneity and resources are predictable
	Mid	Inequality is likely but least probable with a small economy of scale
	Most	Inequality always likely, but least probable with low heterogeneity and no predictability
High	Least	Inequality is very unlikely
	Mid	Inequality rare but most probable when there is high heterogeneity and a high economy of scale
	Most	Inequality is likely when there is high heterogeneity and resources are completely predictable

Table 2. Inequality outcomes. Key conditions for inequality are reported at each monopolizability cost level, with other resource characteristics held at their levels least, mid, or most theoretically likely to favor inequality. Least = little heterogeneity, high abundance, no predictability, and a small economy of scale. Mid = all variables at their middle level. Most = high heterogeneity, low abundance, complete predictability, and a large economy of scale.

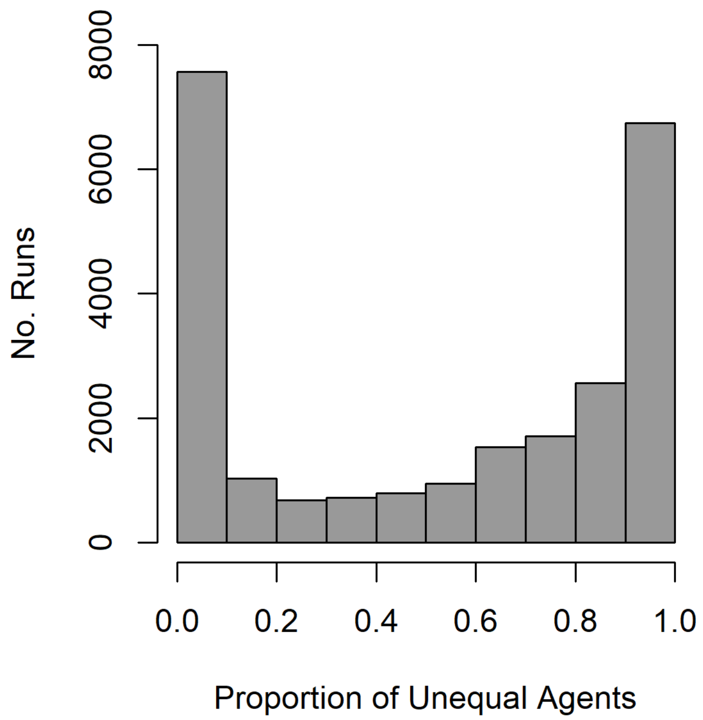

Figure 1. Histogram of proportion of agents employing the unequal strategy across all model runs (n = 24,300).

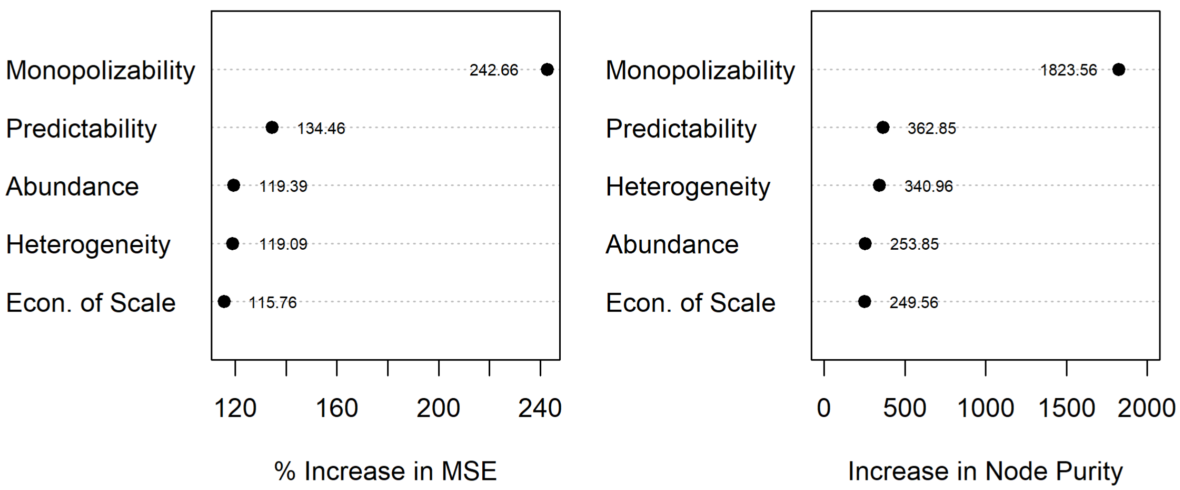

Figure 2. Variable importance from RF regression showing both the percent increase in mean square error (MSE) and the increase in node purity as a result of permuting each variable out of the analysis. MSE increase represents the increase in prediction error incurred by dropping the given variable, whereas node purity is residual sum of squares representing the improvement in prediction of the proportion of agents employing an unequal strategy resulting from splitting the data on the given variable.

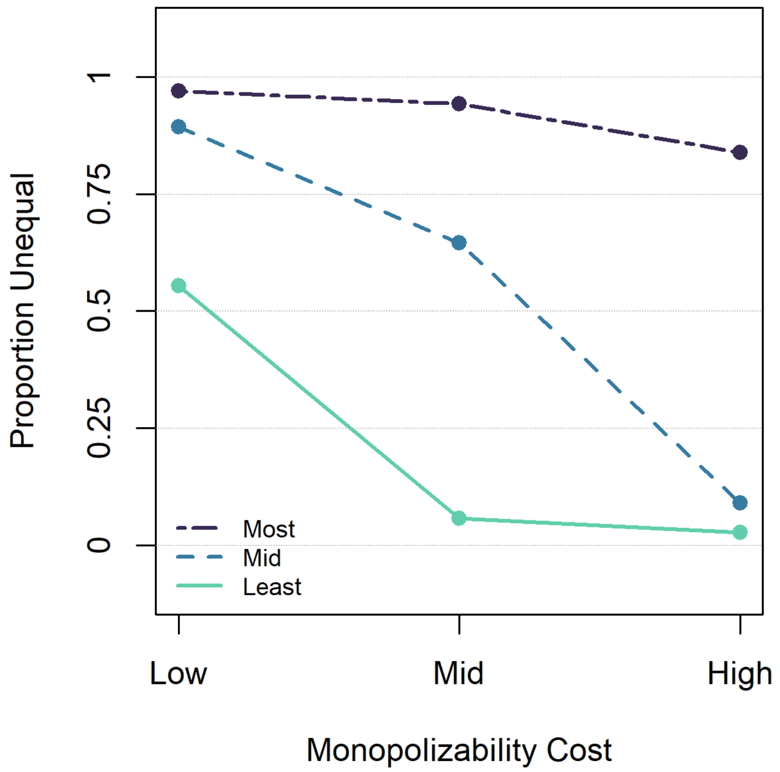

Figure 3. Partial response plot for monopolizability when all other variables are held at their least (teal), mid (blue), and most (purple) likely to promote unequal access values.

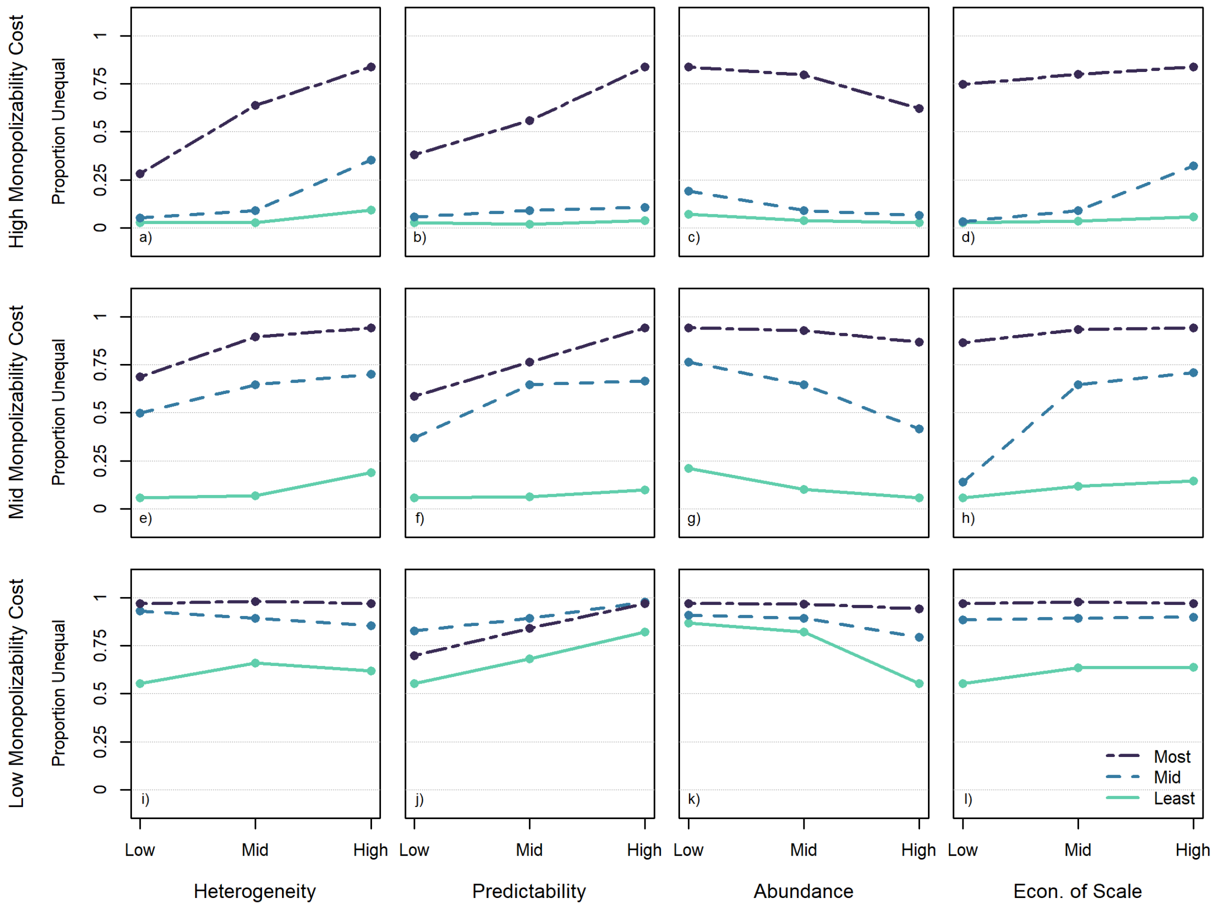

Figure 4. Partial dependence responses for each resource characteristic at each level of monopolizability when all other characteristics are held at their levels least (teal), mid (blue), and most (purple) theoretically likely to promote inequality.

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