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ARTICLE

The Evolution of Inequality

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Understanding how systems of political and economic inequality evolved from relatively egalitarian origins has long been a focus of anthropological inquiry. Many hypotheses have been suggested to link socio-ecological features with the rise and spread of inequality, and empirical tests of these hypotheses in prehistoric and extant societies are increasing. In this review, we synthesize several streams of theory relevant to understanding the evolutionary origins, spread, and adaptive significance of inequality. We argue that while inequality may be produced by a variety of localized processes, its evolution is fundamentally dependent on the economic defensibility and transmissibility of wealth. Furthermore, these properties of wealth could become persistent drivers of inequality only following a shift to a more stable climate in the Holocene. We conclude by noting several key areas for future empirical research, emphasizing the need for more analyses of contemporary shifts toward institutionalized inequality as well as prehistoric cases.

Throughout human history, relatively egalitarian societies have repeatedly and, often independently, developed political and economic inequality, a phenomenon that is apparent in both the archeological[1,2] and ethnographic records.[3–5] How and why inequality emerged and spread has been the subject of much theoretical debate, but no consensus has been reached, and details on the mechanisms of transition to inequality remain poorly understood. Here we evaluate and synthesize various perspectives on inequality relevant to evolutionary anthropologists. We focus on evolutionary explanations of independent emergences of persistent institutionalized inequality (PII) in small-scale, relatively egalitarian societies. Although PII is relevant to cultural evolutionary models of inequality, we only indirectly consider its diffusion or imposition from larger, more complex, and stratified societies.[6] Our explanations center on the relative costs and benefits of inequality to individual reproductive success (RS) or other plausible fitness correlates. This theoretical emphasis facilitates synthesis of disparate ideas and can apply in principle at any point in human history to which the specified context and causal conditions are met.

Because this is primarily a conceptual review of the literature, we focus on models and debates rather than attempting a systematic survey of empirical studies of inequality. We discuss inequality in various extant or prehistoric small-scale societies to illustrate key issues (Boxes 1 and 2). We hope this review will help stimulate and guide future efforts to explore the evolution of inequality in both ethnographic and archeological contexts. Indeed, a clearer understanding of the evolutionary origins and adaptive significance of systems of inequality should motivate increased efforts to document the emergence of inequality *in situ* in ways that generate comparable data across field sites.

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MODELS OF INEQUALITY

At some level, inequality is ubiquitous. In all human societies, different degrees of prestige and power are correlated with individual characteristics such as age, gender, and ability.[7–11] Persistent inequality, however, involves

GLOSSARY

Achieved—achieved differences in power or status are determined by an individual's abilities, performance, or effort.

Aggrandizers—ambitious individuals who actively manipulate others to enhance their own status, power, and well-being.

Ascribed—ascribed differences are assigned at birth or assumed involuntarily through, for example, inheritance of resources or status positions.

Circumscription—where steep resource gradients (rich to poor) or severe social barriers such as lawless zones make emigration very costly, allowing dominants to exploit subordinates with greater intensity or less coercion.

Coercion—control of the behavior of others through threats or attacks.

Collective action problem—any situation in which multiple individuals would benefit from an action, but difficulties of coordination or ensuring fair contribution to the costs of the action create obstacles; also known as a "social dilemma."

Complexity—social complexity can refer to systems with many interrelated parts (for example, ethnic groups, or classes) or to specific traits such as high population density, sedentism, intensive subsistence economies based on food storage, and occupational specialization.

Coordination problem—situations in which individual success requires collective action to achieve a goal; ranges from pure coordination, where individuals have the same preference or fitness ranking across outcomes, to cases in which individuals have different rankings but could still achieve higher payoffs by coordinating on one choice.

Cumulative culture—any system of cultural transmission characterized by gradual (multigenerational) addition of features to existing traits; for example, elaboration of a simple kinship system or additive improvements in a given technology.

Dominants—powerful members of a social group who achieve and maintain this differential through coercion (cf. prestige).

Egalitarian—all human societies exhibit inequalities in power and prestige, but are conventionally termed "egalitarian" if, within gender and age classes, inequalities are achieved (and therefore relatively ephemeral) and access to subsistence resources is equal. In contrast, nonegalitarian societies are characterized by persistent (often inherited) inequalities in power, prestige, and wealth based to a large degree on ascribed roles. ("Egalitarian" has a somewhat different meaning in the animal behavior literature, where it refers to systems lacking dominance structures or reproductive skew).

Gini coefficient—a measure of the degree of inequality in the distribution of resources or some other attribute; there are many ways to compute a Gini coefficient, but it typically varies between 0 and 1, where 0 represents complete equality of resource distribution and 1 represents the hypothetical extreme at which a single individual or household controls all resources.

Hierarchy—group organization in which individuals are ranked by differences in status or power; hierarchy is more transient than stratification and ranks are typically allocated to individuals rather than classes.

Inequality—differential access to power or resources, with persistent differences often resulting from hereditary privileges or formal position; quantitative measures include the Gini coefficient, Lorenz curves, and variation in key resources across individuals or groups.

Mutualism—a form of cooperation that results in higher payoffs to cooperators than either party would achieve alone.

Persistent institutionalized inequality (PII)—differential access to power or resources involving institutionalization of status hierarchies by hereditary privileges or positions such as social classes, castes, hereditary titles, or heritable differences in wealth.

Population pressure—the ratio between population density and the density of available resources.

Power—the ability of dominants to motivate subordinates to behave in ways they would otherwise not, often but not necessarily through coercion.

Prestige—influence or deference that is freely granted rather than through use of threat or force.

Small-scale society—a society consisting of one or a few communities, each containing from several dozen to a few hundred individuals; with some notable exceptions, these tend to be egalitarian.

Status—the relative degree to which an individual is admired or respected by others in the social group; also, an individual's place in a social hierarchy

Stratified societies—those having well-defined divisions (castes or classes) with low mobility between strata and high degrees of inequality in wealth and power.

Subordinates—less powerful members of a social group.

Transegalitarian—societies exhibiting some degree of ascribed and persistent but relatively muted or constrained inequality; such societies are generally small in scale and may have relatively minor degrees of wealth inequality.

Box 1. Empirical Applications in Ethnographic Research

We have reviewed arguments that a shift to a relatively stable Holocene climate was the main environmental factor allowing the emergence of PII in human evolutionary history. Yet this explains neither what drives the marked cross-cultural variation in the emergence of PII nor any trends toward greater egalitarianism in past or contemporary settings. Qualitative studies reviewed by Gurven and coworkers[112] show considerable variation in the extent to which increased material wealth enhances or erodes traditional sharing networks, in turn affecting the extent to which these factors are associated with economic inequality. Expanding on Gurven and colleagues'[112] reasoning, we suggest that variation within and among populations in the development of PII hinges on the extent to which novel forms of wealth are economically defensible and transmitted across generations and the strength and persistence of traditional sharing norms and institutions. Forms of wealth that are relatively impermanent, used primarily for signaling purposes (such as many luxury goods), or subject to theft should be considered relatively indefensible and unlikely to be transmitted across generations. Therefore, they are less likely to lead to PII. The extent to which egalitarian sharing norms and institutions successfully resist increases in PII is likely to depend on the specific benefits such norms provide (for example, whether they enhance social capital or buffer against material losses). Work among the Tsimané and !Kung illustrates these two points.

The Tsimané, forager-horticulturalists residing in semi-sedentary bands in lowland forests and savannas of Bolivia, have, since the 1970s, become increasingly involved in the local market economy.[113] In this context, the Tsimané Health and Life History Project has led to intriguing findings[112,113] that exemplify how contemporary ethnographic research may provide insights into the emergence and drivers of inequality. Researchers associated with this project explore how market integration, which provides both access to novel forms of wealth and acculturation to mainstream Bolivian cultural values, has affected the health, wealth, and inequality of an otherwise economically self-sufficient community of indigenous people. Centered in the Spanish-speaking town of San Borja, the market economy has penetrated Tsimané life styles to different degrees, based, in part, on proximity of residence to San Borja,[113] access to roads, and fluency in Spanish.[78] That behavior change and acculturation have occurred in response to market integration is clear, as shown by strong preferences to use cash to buy status goods.[112] At the same time, the effects of market integration on subsistence patterns have been relatively weak, as the Tsimané have, by and large, continued to rely on traditional means of making a living (fishing, hunting, gathering, small-scale farming).[113]

Does the incipient influence of the market economy among the Tsimané lead to increased inequality? In contrast to expectations, detailed data on different types of wealth and sharing behavior at individual, household, and community levels have shown increased evidence of wealth redistribution as individuals and communities experience greater levels of market integration.[112–114] There may be several reasons for this apparent contradiction. 1) The forms of wealth provided by the market were perhaps neither economically defensible nor readily transmitted. The measure of "market wealth" provided by Gurven and colleagues included "industrial assets," "domestic animals," and "traditional assets"; these were amalgamated to produce a measure of overall household assets in Bolivian dollars. Plausibly, focusing on more easily transmissible material capital "'industrial assets" or specific forms of wealth known to be transmitted with high fidelity across generations; durable versus consumable goods) would have shown a stronger associated pattern of wealth differentiation. Gurven and colleagues also note that "cash and material goods are subject to theft," suggesting that procured goods were economically indefensible in the absence of institutionalized means to protect them. 2) Conforming to existing norms of redistributing wealth may provide better insurance against misfortune, such as crop loss or illness, than does self-insurance through accumulating market-derived wealth, at least in cases such as this, where individuals have only a "weak toehold in the market economy."[115] Such conformance to norms of reciprocity could also be motivated by sanctions from other community members who resent hoarding of market goods.[114] (3) Sharing maintains social partnerships that can be important to the production of market goods and acquisition of political influence. Allies are important for obtaining access to prime cash cropping locations, for labor assistance, and favorable negotiations with merchants.[88] Socially-connected and economically successful individuals are likely to wield more political influence,[89] which may be due in part to increased demand for leadership in the face of market-related conflicts[78] and to increasing patron-client relationships within Tsimané villages.[112]

Research among Kalahari hunter-gatherers provides insights into the process of norm replacement as egalitarian societies encounter new forms of wealth and livelihood. Examining the !Kung San (Ju/hoansi) as they became

increasingly involved with part-time herding and trade in market goods, Yellen[116] noted three distinct transformations in norms and practices: a decline in sharing as people with such goods "started hoarding instead of depending on others to give them gifts"; a reduction in mobility due to increased material possessions and tethering to sources of goods such as Bantu cattle camps, trading posts, and settlements with government services; and a shift from exterior hearths and open-door brush huts facing each other to interior hearths and "semi-permanent mud-walled huts [that] faced away from one another." These factors were mutually reinforcing in fairly obvious ways: Accumulated material wealth impeded mobility, as did mud huts, while the privacy the latter provided reduced demand sharing, in turn facilitating wealth accumulation. Reduced mobility "fueled still more change, in part because the people could no longer resolve serious arguments in the traditional manner, by joining relatives elsewhere...." and "turned [instead] to local Bantu chiefs for arbitration." Thus, political inequality within !Kung society was not directly institutionalized, in part because external authorities (bureaucrats as well as Bantu chiefs) were sought out to manage common disputes.

Cultivation and livestock herding show how tensions associated with privatization arise between those who have begun to farm and herd and others, often relatives, who continue to subsist by foraging. As Biesele and coworkers[117:123] noted, "When a !Kung family harvests or comes into possession of livestock, they come under intense pressure to share their good fortune with their kinfolk and affines. If they give in to these demands their stocks are depleted rapidly below the point of economic viability, whereas if they refuse, they are accused of stinginess, a serious social stigma." In essence, the problem facing incipient farmer/herders in an egalitarian foraging society is to legitimize new norms and institutions involving private property, surplus accumulation, and reinvestment.[55]

More detailed ethnographic case studies are necessary before we can draw firm conclusions about how PII arises or reverses in a given locale. Our review suggests several directions for such research. First, these studies should use strong quantitative methods, complemented by qualitative data to ground hypotheses and inform conclusions. Without this complementarity, quantitative data would have limited ability to refine hypotheses. For example, the proportion of kin versus nonkin participating in exchange networks and the degree of marital assortment within a community undoubtedly affect the evolution of PII.[118] While these data can be collected systematically using quantitative methods, establishing the need for them would be impossible without qualitative understandings of social dynamics in a given site. Second, such methods should allow resolution of the scales within households or communities or between communities, at which PII emerges.[112] Further work will be required to assess the degree to which inequality driven by increased market integration ratifies the causal importance of defensible resources and wealth transmission summarized in this review.

institutionalized hierarchies that go beyond such personal characteristics or family roles.[12] The high levels of institutionalized inequality common in many modern and historical state societies evolved from relatively egalitarian origins in the terminal Pleistocene or early Holocene,[1,13] and initially affected relatively few societies.[14] Our focus here, as in much of the literature, is on PII. Why do so few relatively egalitarian societies remain in the modern world? What causes underlie the seemingly ubiquitous, but not unidirectional[15] transitions occurring at disparate times and places?

Many answers to these questions have been posited and, given the variety of theoretical frameworks from which these explanations emanate, no consensus yet exists. It is beyond the scope of this review to provide accounts of each of these proposed explanations. Instead, we construct a possible synthesis by identifying factors that underlie associations between other variables hitherto considered to be causal in their own right. We deal only indirectly with explanations that emphasize technological innovations,[4,16] intergroup conflict over resources, and the cultural transmission of inequality within[9] or across societies.[6] In our view, such explanations, by focusing on the population-level emergence of inequality, leave unanswered the fundamental question of how individual strategies adjust to allow for the evolution of inequality. In contrast, the adaptationist perspectives[11,17,18] that we advocate centralize the costs and benefits to individual actors within their social systems, yielding a more coherent and, we argue, accurate understanding of the forces that act directly to generate inequality.

We deal more directly with arguments that have focused on broad ecological shifts as the basis for widespread inequality, but assign these a more peripheral role. We argue in detail that population pressure,[19,20] which is commonly associated with inequality, is insufficient to generate it in the absence of differential control of productive resources or other important forms of wealth that can be transmitted to descendants. Similarly, although agriculture is often thought to produce inequality,[21] we note several counterexamples, including the existence of egalitarian small-scale horticultural societies with extensive land use,[22] as well as persistent inequality in purely foraging economies, as exemplified by cases in western North America,

Box 2. Empirical Applications in Archeological Research

Given that many empirical observations relevant to PII are of the prehistoric record (for example, monumental architecture, burial wealth, dwelling size) and that their temporal depth greatly assists in inferring causality, archeology is well positioned to investigate the key drivers of PII, albeit at a population level rather than in terms of individual action and consequences. Successful archeological explanations of PII should describe variation in defensible resources, identify the associated archeological signature of inequality, and demonstrate how a particular key driver links resources and the origin of PII in each case.

Various archeological studies have described the temporal and spatial variation in defensible resources. These are primarily focused on either agricultural resources[119,120] or dense, spatially concentrated wild resources.[38,121] The former type of study is exemplified by a multi-disciplinary project on the prehistory of Rapa island in southeast Polynesia.[122] Coordinated analyses of plant microfossils, radiocarbon dates, agroecology, remote sensing, and earthwork surveys indicate that introduced taro (*Colocasiae sculenta*) cultivation began almost immediately after human colonization, circa AD 1200. Within 100 years, fortified villages were constructed overlooking the most productive lands as pondfield agricultural system expansions increased the value of land that was both highly circumscribed and defensible.[123] There are fewer studies describing defensible wild resources. Work on the California Channel Islands, summarized by Kennett,[124] details the chronological and spatial variation in marine mammal and fish resources associated with different catchments. Using zooarcheology, marine biology, and paleoclimate analyses, Kennett notes that rich marine resources varied in distribution and productivity over space and time.[124] Such studies demonstrate the utility of multi-disciplinary tools, often including paleoenvironmental, zooarcheological, archeobotanical, chronological, and landscape survey components, in describing temporal and spatial variation in defensible resources.

Direct evidence of gradations of inequality, albeit difficult to identify archeologically, is informative regarding the origins of PII. Mitigating this difficulty, Ames[98] has argued that differential access to basic and prestige resources is key to studying PII. Basic resources associated with subsistence are readily identified as described earlier, and through human skeletal analyses.[125] Prestige resources are identified through the spatial and contextual (for example, residential or ritual) distribution of materials with respect to their rarity or some measure of material quality or cost.[126] While differential access to prestige resources indicates inequality, differential access to both basic and prestige resources indicates PII. An example of differential access to prestige resources comes from Kirch and colleagues,[127] who analyzed the context in which local basalt artifacts from east Maui and exotic basalts from other islands were found. Exotic basalts sourced to the Mauna Kea quarry on nearby Hawaii Island were found in temple or elite residential contexts twice as often as in residential contexts, suggesting that "control over access to and distribution of these stone resources was controlled by elites."[127] In a related analysis, Ladefoged, Lee, and Graves[128] examined a contemporaneous agricultural system on Hawaii Island. Elite managers (chiefs) controlled the production and distribution of agricultural resources by dividing the 60-km^2 dryland farming system into an increasing number of independent parcels. This division maximized surplus agricultural production controlled by elites, but lessened the estimated life expectancy of populations within parcels. Combined, the research by Ladefoged and Kirch and their coworkers documents the presence of PII with the differential access and control of both basic and prestige resources by a subset of the pre-contact Hawaiian population.

Many archeological studies describe variation in defensible resources and identify the archeological correlates of inequality. Fewer studies[73,129] have combined these with investigation of the processes or drivers that explain the origins of PII in particular cases. This seems to reflect the difficulty of the archeological task. Precise chronological and spatial control of multiple data types across different domains is required. Prentiss and colleagues'[67,68] research in the Middle Fraser Canyon, British Columbia, discussed in the section on population pressure, is one example where the necessary data types, chronological control, and theoretical framework are brought to bear on the origins of PII. Village sites occupied by complex hunter-gatherers contain variably sized pit-house dwellings that can be precisely dated, with assemblages that are plausibly the results of household-level (that is, kin-based) behavior. Fine-grained subsistence and paleoenvironmental data indicate the range in defensible faunal resources used, variation in resource control by households over time, and episodes of resource stress, while artifact assemblages depict different quantities of prestige goods (such as groundstone pipes). Although there is variation across the sites of the Middle Fraser Canyon, it appears that after 1,000 years of prior occupation, PII emerged as specific households exercised relatively greater control

of prime salmon fishing spots in a regional context of increased resource pressure, then increased their accumulation and transmission of material wealth. In one of the very few archeological uses of a quantitative index of wealth inequality, Schulting[130] calculated Gini coefficients for mortuary wealth objects in a broad sample of sites in the same region; these ranged as high as 0.7, equivalent to wealth inequality in the most unequal societies of the modern world.

Florida, coastal New Guinea, and elsewhere.[16,23–25] While we agree that there is an increased likelihood of PII in societies that practice intensive agriculture using plows, animal labor, and irrigation,[26] we see agriculture as corollary rather than causal.

Our synthesis is organized around several key questions. First, what appear to be the main social and ecological factors consistently associated with and arguably driving the evolution of PII? Second, how do these drivers account for the relationship between population and resource pressure and PII? Third, why is PII tolerated and who stands to gain from it? Fourth, why does PII arise so late in the archeological record?

WHAT DRIVES THE EVOLUTION OF PERSISTENT INSTITUTIONALIZED INEQUALITY?

As noted, various factors have been proposed as key determinants of the rise of PII. Here we focus on three — the resource base, intergenerational wealth transmission, and population pressure — that our review of the literature identifies as currently being the most widely advanced, while also discussing additional factors that figure less prominently but are related to these key variables.

Defensible Natural Resources

In nonhuman societies, forms of inequality such as dominance relations and reproductive skew are often linked to differential control of resources,[27] a pattern also commonly found in anthropological analyses of the emergence of inequality. Two questions immediately arise concerning this argument. Why does differential control of resources arise in some times and places and not others? And why do individuals allow some members of their group to exercise such control? Theory from evolutionary ecology can usefully address these questions.

Economic Defensibility

For at least half of a century, evolutionary ecologists have analyzed the evolution of resource control in terms of the trade-off between the fitness benefits of controlling resource patches and the fitness costs such control entails. Benefits can accrue through increased resource consumption or mating success, whereas costs arise from the time, energy, and risk of injury entailed in monitoring an area, advertising one's presence, and deterring intruders.[28] The basic principle, known as economic defensibility, is that natural selection would favor resource control behaviors such as territorial defense only if their fitness benefits exceeded their costs.

Although resource values and defense costs vary along several dimensions, in many cases the spatiotemporal distribution of resources — specifically, their density and predictability — are key. Dense resources are more likely to repay the costs of territorial defense because the area to which one must control access for a given level of resources is smaller, entailing less time and effort in monitoring and advertisement. Predictable resources are more defensible because the area that must be defended to encompass them is easier to locate and the income (resource consumption) from the area is more reliable. Importantly, the costs and benefits of controlling access depend on the resource user's capabilities (for example, birds can fly and advertise territorial claims with song). In the human case, these capabilities include technologies for transport (such as watercraft) and harvesting of resources,(such as scythes), as well as culturally variable traits such as social norms and institutions (for example, rules governing ownership and inheritance).

Although the economic defensibility (ED) model is simple, it has helped biologists explain broadly diverse territorial systems and has been validated in hundreds of studies of spatial behavior in a wide variety of species.[28–30] This model also provides a means of understanding the associated emergence of persistent institutionalized inequality (PII). Assessments of the ED model in various ethnographic, ethnohistoric, and archeological contexts[31–34] point to three broad conclusions: (1) human territorial behavior (exercising spatial ownership claims, controlling access to resources) is facultative and varies strategically; (2) this behavior corresponds to variation in resource density and predictability across space and time; and, (3) since ED can vary by resource, control of access within the same social system can be applied to some resources but not others.

Several cases suggest that these features (density, patchiness, predictability, and individual attributes facilitating defense) are key to operational definitions of ED. Resources harvested by many hunter gatherers are unpredictable in space and/or time: a caribou herd is mobile and best hunted opportunistically[35]; grass seeds in arid settings vary in location and abundance from year to year.[36] On the other hand, some wild resources, such as salmon streams in the Pacific Northwest, acorn groves in Native California, and furbearing animals on subarctic trap lines, are dense and predictable enough to warrant territorial claims.[33] In these and other cases, however, ED depends as much on behavioral and

cultural factors, including technology, as on environmental ones. Salmon are effectively a much denser resource if trapped in weirs and preserved for storage, while acorn groves are much more defensible once processing and storage technology is developed. Among horticulturalists, garden plots are defended, but uncultivated bush is usually is not,[22] since land supply generally exceeds demand. Strong property rights, and with them PII, explode with the spread of more intensive agriculture.[37] ED considerations provide one reason why this would be true, as agricultural intensification greatly enhances resource density and predictability.

The vast majority of territorial animal species are solitary or live in pairs, each with its own territory, and lack anything resembling PII. Similar conditions prevail in some small-scale human societies, with family groups or hamlets each controlling equivalent resource patches and exercising relative autonomy and self-sufficiency. Thus, resource defense in itself does not produce PII. ED must be accompanied by conditions that allow some individuals to control more resources than others and to use this differential control to institutionalize inequality.

Illustrating this point, Bettinger[38] found that in many California Indian societies "ownership of key resource patches by small kin groups" was the norm, although some resources were collectively owned by the village or multi-village "tribelet." Bettinger attributes the spread of this institutional pattern to the reliance on plant resources such as acorns, pinyon nuts, and grass seeds, which were (1) abundant, predictable, and evenly distributed (rather than clumped), but (2) required extensive postharvest processing. The features listed in (1) clearly match ED model expectations of defensibility at a localized or family scale, while precluding differential control of key resources by a subset of these families; in these societies, every family group could control and subsist off their own resource patches. Feature (2) is less critical, but reduces motivation to usurp resource patches of others.

In contrast, highly concentrated (patchy) distributions of dense and predictable resources such as the salmon aggregations at river mouths and rapids along the Northwest Coast can be economically defended by fewer people than can subsist on the patch. Because the "owner" subgroup grants resource access to subordinates in exchange for labor in harvesting, processing, and defending these resources, as well as other services, this uneven distribution of defensible resources allows the emergence of PII. Thus, in both the acorn-based economies of California and the salmon-based economies of the Northwest Coast, resources are economically defensible. The emergence of PII in the latter communities is a result of the highly clumped resource distribution, which allows differential control.

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ED, like many models in evolutionary ecology, emphasizes generality rather than realism or precision; it predicts that resource defense will occur when its costs are less than the benefits of increased control (that is, when defense is profitable). As noted, many factors can affect these costs and benefits; it would be fruitless to attempt to enumerate them all. In addition, the social scale of resource control can vary from individuals or family groups to corporate groups (such as clans), villages, or larger units. Increasing the size of the group defending resources has obvious advantages, and may be one potent driver of increasing the size of communities and polities over time.[1,2,39] However, group defense raises significant collective action problems that must be solved in order for it to emerge and be stable against free-riding;[30,32] for various reasons, humans have been much more successful at solving such dilemmas than most other species.[40] At the same time, many cases of group defense entail unequal allocation of costs and benefits, which may underlie the emergence of PII. We will examine this issue further, along with other aspects of the means by which control over resource patches is established. However this control occurs, the resulting system of ownership leads to the intergenerational transmission of wealth, a process that has its own characteristic dynamics and effects on inequality.

Material Wealth Transmission

Individually owned and heritable wealth can have major impacts on reproductive success (RS),[41,42] creating a clear evolutionary rationale for links among economic defensibility, intergenerational wealth transmission, and PII.[43] Recent attempts to understand the evolution of social inequality from an evolutionary ecological perspective have thus focused on three elements pertinent to understanding the unequal distribution of wealth: the relative impact of different types of wealth on well-being and lineage persistence; the transmissibility of wealth across generations; and the properties of different wealth types that affect how easily they can be monopolized and transmitted.[13,14,22,44–47]

Given that inequality often arises in societies where material wealth is basically absent, we use a broader definition of wealth than is incorporated in typical social scientific analyses of inequality. *Sensu* Borgerhoff Mulder and coworkers,[44] we understand "wealth" as any of a broad array of factors that are transmitted to offspring and can affect an individual's health, well-being and RS. As such, wealth can be subdivided into material (such as capital assets, land, livestock); social or relational (the network of individuals available

to support one's interests); and embodied or somatic (such as skills, knowledge, and health-based differences in well-being[48]). Different forms of wealth are emphasized differently within and among societies based on the ecological context and subsistence base,[14] and on the norms and institutions that legitimize property and inheritance rights.[49]

Though embodied and relational forms of wealth are heritable and associated with moderate degrees of inequality, material wealth is especially conducive to supporting inequality[14,22] because the costs of defending it are more readily outweighed by returns in RS.[49] Recent research by Borgerhoff Mulder and colleagues[44] has found that the scope of inequality was greater in pastoralist and agricultural societies than among foragers or horticulturalists because of their greater reliance on heritable forms of material wealth such as land and cattle. Thus, even in forager or horticulturalist societies where embodied and relational forms of wealth form the mainstays of subsistence, newly available forms of material wealth can quickly become more important and support higher levels of inequality than do preexisting traditional forms of wealth (Box 1).[50] In addition, material wealth is highly associated with RS in a variety of societies,[50,51] although these results are much clearer for men than women,[51] which may produce gendered differences in the evolution of inequality.[43]

As alluded to earlier, the relationship between wealth and inequality varies among different types of material wealth.[11,49] While some forms of wealth, such as food stores), are easily depleted, others have the capacity to generate further wealth[52] and do so at different rates.[49] Domesticated animals, for example, reproduce at higher rates than do human populations, allowing for distribution among several sons, but herds must be maintained above threshold levels to ensure long-term viability in the face of environmental disasters.[41,52] Land productivity cannot be increased as rapidly as livestock, and thus cannot continue to be subdivided among heirs across generations. This leads to rules limiting inheritance (for example, unigeniture), a strong potential for inequality within families, and dispersal of noninheriting offspring.[53]

Attempts by lineages to monopolize material wealth may be circumvented or bolstered by social norms and institutions.[11,44,49] The highest rates of intergenerational wealth transmission and inequality occur in pastoral and agricultural societies,[14] where rights to resources are often relatively permanent and exclusive in association with intensified labor put into the production of material resources.[49] Socially enforced monogamy is often characteristic of agricultural societies, perhaps to prevent land from being divided among many sons, whereas polygyny in pastoral societies benefits sons with growing herds of livestock.[49] Endogamy[17] and positive marital assortment[14] facilitate the monopolization of wealth within lineages, practices found even among some densely populated foragers with transmissible wealth and defensible resources.[54]

In summary, different forms of wealth vary in their effects on RS and the degree to which they are transmitted to offspring. The relative defensibility and potential fitness returns of material wealth make it especially suited to supporting social inequality, even in societies where its importance is newly emerging (Box 1). Social norms and institutions can change quickly to accommodate novel forms of wealth, but egalitarian social norms and leveling mechanisms can, if they persist, also act as strong impediments to the monopolization of wealth.[55,56]

Several key questions remain regarding how different types of wealth structure the evolution of inequality. First, the degree to which each type of wealth interacts with others in generating overall levels of inequality is poorly understood.[14,50] Analyses have recognized the interdependence among wealth types,[13,44,47] but its precise nature remains to be elucidated and may vary across societies. Second, the measurement of wealth is tricky, not least because the forms of wealth most important to RS and well-being vary significantly across locales.[14,44,50] Though it may be possible to isolate a single form of wealth as most critical to RS (for example, camels among the Gabbra[52]), it is more likely that many forms of capital and noncapital assets need to be considered simultaneously.[50] Thus, while an evolutionary ecological framework may generalize sufficiently across societies to support specific hypotheses about the relative importance of wealth types in structuring inequality, comparability across a given measure of wealth, such as land, may be limited. Finally, scholarship in archeology has provided some of the strongest evidence of the emergence of inequality, but the ability of that evidence to identify private ownership and unequal allocations of wealth is limited (Box 2).[49] Phylogenetic analyses may be helpful in reconstructing historical patterns of resource inheritance, norms, and institutions[57] to supplement these gaps in archeological and historical evidence.

Population and Resource Pressure

Evolutionary ecology models suggest that competition for a given resource affects its value. It is no wonder, then, that population pressure on resources has long been featured in accounts of the evolution of inequality (though this view also has many critics).[8] The debate has not been helped by varying definitions or conceptions of the term, in particular tendencies either to conflate population pressure with the more easily measured population density, or to link either to the dubious concept of a fixed carrying capacity.[58,59] Keeley[20] defined population pressure as "the ratio between population density and the density of available resources," which is reasonable, given some means of measuring resource density. Archeologists often use proxies, such as evidence of nutritional stress (for example, Harris lines in long bones) or resource scarcity (for example, extensive processing of prey material to extract marrow or bone grease).

Perhaps the most ambitious attempt to test the argument that population pressure leads to institutionalized inequality is that of Keeley,[20] who examined 94 ethnographically described hunter-gatherer societies. This effort involved a complicated set of measures and indices of environmental-resource variables and four measures of "social complexity": residential mobility, food storage, use of exchange media (such as shell money), and a coding for class distinctions from the *Ethnographic Atlas*.[60] Since low mobility and food storage are strongly correlated with population density, if not pressure, and exchange media are somewhat of a side issue, we are most interested in Keeley's results for the relationship between population pressure and class distinctions (termed "social inequality").

Keeley incorporated primary productivity (that is, the amount of terrestrial plant biomass produced per unit time) in his measures of resource density, arguing that deviations from the regression of productivity on population density indicate the degree of population pressure. However, given that human diets depend on specific resources and microhabitats rather than overall plant productivity, primary productivity can be a poor predictor of food availability. In Keeley's analysis, the Chumash of coastal southern California exhibited the greatest positive deviation from the expected population density given local primary productivity and were ranked high in social complexity, whereas the Guayaki (Ache), in lowland tropical forests, had the greatest negative deviation and low social complexity. While Keeley interpreted such results as corroborating the effects of population pressure, they could instead be due to the fact that Guayaki inhabit an area where most primary productivity (woody plants) is poorly correlated with available resources (primarily game and honey), whereas the Chumash had relatively dense marine resources to exploit, which are not included in Keeley's primary productivity measure.

In direct contrast to population-pressure explanations, others[61–63] argue that complexity and inequality are driven by per capita resource abundance, which fuels competitive feasting, surplus accumulation, and patronage on the part of ambitious "aggrandizers." These studies propose individual desire for power or status as the "engine of change."[61] Earle,[62] for example, ascribed the origin and development of inequality in ancient Hawaii to individuals who directed the distribution of agricultural surplus produced from simple, community-built irrigation facilities (Box 2). Inequality increased as particular individuals gained greater control over this surplus.

A middle way between the population-pressure and resource abundance arguments is offered by analyses focusing on competition over dense and predictable (that is, economically defensible) resources that allow differential control and the emergence of patron-client relationships and other forms of institutionalized inequality.[64–66] Research by Prentiss and coworkers[67,68] at prehistoric salmon-fishing villages in interior British Columbia exemplifies this approach. Here, the emergence of inequality was associated with declines in salmon and deer populations, as well as human demographic contraction, rather than with any major technological changes or expansions in per capita food storage. Ethnographic accounts from the same area[69] indicated that households were headed by chiefs who claimed ownership of key fishing and hunting sites. Prentiss and coworkers[67,68] conclude that successful households responded to resource competition by tightening their control of key resource sites, then allowing others to co-reside as subordinates, managing their labor in ways that allowed them to accumulate wealth and hosted feasts (signals of success that in turn attracted allies as well as additional subordinates). This study illustrates the distinction between resource abundance (amounts per capita) and resource density (amounts per unit area). Salmon remained a relatively dense (and predictable) resource even as their abundance declined. More importantly, this study highlights the importance of explicitly delineating the causal mechanisms and evolutionary processes that might link population-resource balance and social phenomena such as inequality and resource control.

Making an explicit link between natural selection and PII, Vegvari and Foley[70] present an agent-based simulation in which the probability of sexual reproduction by mature agents is linked to mate availability and an agent's energy budget as determined by the availability of up to ten different subsistence resources. Importantly, agents innovate or learn up to ten cultural traits, each allowing access to one of the ten subsistence resources. In turn, resource pressure is partly linked to trait innovation and the number of traits in a population. Cultural trait innovation may either allow access to a new resource or make existing resource use more efficient. Vegvari and Foley demonstrate that even in small, isolated populations, under certain conditions such as high selection pressure and low innovation costs, resource pressure can play a larger role than population size and resulting transmission biases in increasing the number of traits in a population, one measure of cultural complexity.

Such research suggests that sophisticated analyses of the emergence of inequality guided by models from evolutionary ecology can avoid unproductive dichotomies between "population pressure" and "resource abundance" arguments. Under some circumstances, population pressure may be important in the emergence of PII, but it is neither necessary nor sufficient, and is probably too widespread to explain the patterns of differential emergence and timing of PII seen in the empirical record.

WHY TOLERATE INEQUALITY?

The arguments reviewed suggest that, irrespective of the degree of population pressure, differential success in competition over valued resources interacts with economic defensibility and intergenerational

wealth transmission to generate PII. But who benefits under these conditions, and why? Theorists differ on whether benefits accrue to elite individuals to the net detriment of others or whether most individuals benefit, albeit to different degrees. A related debate concerns whether, to what extent, and under what conditions the evolution of inequality has involved coercion. We consider this question first, then ask whether certain attributes characteristic of leaders in egalitarian or transegalitarian[8] societies position these leaders to establish PII under the right conditions. As a possible means of linking individual attributes to the broader dynamics producing PII, we conclude this section by reviewing arguments positing cultural group selection mechanisms for the emergence and maintenance of social inequality.

Mutualism versus Coercion

Control of dense, predictable resources provides obvious benefits for "owners," even net of defense costs, but why do others allow such differential control? Early analyses of PII tended to emphasize either mutualism, in which everyone benefits from hierarchy (classical functionalism), or coercion, in which one segment of society exploits another against the latter's best interests (classical Marxism). More recent scenarios, as outlined here, tend to fall somewhere along the continuum anchored by these two extremes.

As discussed, ED can result in sustained inequality if some individuals can succeed in controlling dense, predictable resource patches. However, lacking extensive resource storage or durable wealth to buy resources or hire labor, owners (aka dominants) are vulnerable to episodes of injury, illness, and temporary poor harvests. Thus, social ecologies with high mobility, extensive risk reduction through food-sharing, or other conditions creating mutual dependence militate against inequality based on resource control. As many ethnographers have documented, claims to ownership are often contested, and only very stable ecologies with good opportunities for self-insurance by dominants can sustain such claims.[55] But again, ownership, even coupled with stable transmission to heirs, does not in itself amount to PII; this requires differential ownership. How and why does this emerge?

Reproductive skew models[27,71] recognize that per-capita resource access can be equalized in an "ideal-free distribution" even when dominants establish control over certain resources if subordinates emigrate to other locations.[72–74] But when resource gradients are very steep or other factors exist (for example, heightened vulnerability to enemy attack) so that emigration yields even poorer fitness returns than remaining as a subordinate, the resulting circumscription[75] can stabilize inequality based on differential resource control. In effect, subordinates accept their inferior status in exchange for some access to resources, because they are unable to better their lot by emigrating.[64] This argument is formalized in a variety of reproductive skew models.[27,71] Kennett and colleagues[73] employed reproductive skew theory to frame their analysis of the emergence of social hierarchy among the Chumash. In essence, they argued that social hierarchies arose when habitat saturation due to population expansion made it too costly to emigrate and found new settlements; the resulting resource competition forced some (subordinates) to yield power to others (dominants). A related approach, the patron-client model,[64] has been formalized in game-theoretic form, as well as through agent-based simulation; it views the emergence of inequality as a process by which territorial patrons exchange resource access for services from resource-poor clients.[66,76]

The dilemma of leadership, as with inequality, is gaining ascendancy over others while simultaneously winning their approval.

Smith and Choi[66] used agent-based and game-theoretical models to explore factors producing PII involving either "patron-client" systems or "managerial mutualism." Their patron-client model established resource patchiness and spatial variation in productivity as preconditions for generating long-run inequality. Initial advantage accrues to individuals who control a highly productive resource patch and exchange some of their resources with other less well-endowed individuals in return for labor or other support. Thus, patron-client systems[64,66] can emerge when clients accept subordinate positions via interactions with wealthier patrons as the best available choice. Technological innovation can also favor increased monopolization of status and wealth by elites, as among the Chumash of the central California coast, among whom hereditary chiefs financed and controlled the planked canoes used to trade between the mainland and the Channel Islands.[25,54,77] In fact, the need for differential control of resource patches posited in the patron-client model can be generalized to include control of trading networks, specialized technology, or any other defensible resource that contributes substantially to subsistence.[32] However established, once inequality is institutionalized, patrons can use their economic power to bolster their position, through alliance formation with elites in other groups, controlling nonkin labor through hire or slavery and other means (all evident in Northwest Coast Indian societies,[54] among others).

In managerial mutualism,[20,66] one or a few managers facilitates aspects of production, consumption, or information flow. For example, managers may be particularly adept at enforcing cooperation by monitoring and punishing free riders; other cooperators will benefit by each paying a small managerial fee in return.[66] Demographic variables

affect the payoffs to management so that it can be more beneficial in solving collective action problems as, for example, group size increases.[65]

The question of whether coercion or mutualism is more important in the evolution of PII is related to the issue of whether leadership arises from dominance- or prestige-based acquisition of status. The dilemma of leadership, as with inequality, is gaining ascendancy over others while simultaneously winning their approval.[78] Dominance and prestige are arguably distinct pathways to achieving this; dominance arises by inflicting costs on others, whereas prestige is accrued through conferring benefits.[79] Though both can be present simultaneously within the same society,[80] theory and data suggest that prestige is the more common pathway to power in prestate societies.[79,81] Until elites are able to gain effective superiority in weapons and henchmen, "those who pursue self interest with no communitarian considerations often have a quick, brutal demise."[11]

Attributes of Emergent Elites

These models provide an important link between the social and ecological conditions that produce PII and the dynamics between classes of individuals within unequal systems. While the question of who, specifically, stands to benefit from leadership or dominance remains a subject of debate, ethnographic examples of leadership in small-scale societies provide several clues.

Specific qualities seem to characterize leaders in egalitarian and transegalitarian societies (see Smith and coworkers[82] for review), including task-relevant knowledge,[83] productive ability,[84] generosity,[85] age (as a proxy for expertise or knowledge), height, strength, and other traits associated with physical dominance,[86] oratorical abilities, and other forms of "charisma."[87] Leadership is aided by social support from kin and nonkin in small-scale societies,[78] and by perceived trustworthiness, in order to overcome the fear of exploitation.[78,88] Phenotypic correlation (that is, the probability that certain phenotypes are more likely to co-occur in certain individuals) might simultaneously endow emergent leaders with many of these characteristics simultaneously; for example, strength may contribute to both productive ability and dominance, or age may contribute to both task-relevant knowledge and greater effectiveness in oratory.[78,88] Many of these traits have also been implicated as means whereby individuals contribute to the collective.[89] For example, a goal of enhanced reputation may be to motivate disproportionate investments in collective action because reputation increases access to critical support during times of need.[90] This suggests the intriguing possibility that the very traits that support cooperative behavior in risky socio-ecological settings (for example, hunting to reduce the risk of nutritional shortfalls) lead to self-aggrandizing behavior when those settings become more stable and productive.

systems of dominance and coercion are by no means rare in human history or the modern world, suggesting that initial footholds based on prestige and mutualism may be converted to dominance and coercion-based inequality in situations entailing decreasing alternative options for subordinate individuals.

Research to date thus suggests that certain individuals possess traits that enhance their status and leadership. Although opportunities for leadership are often transient in egalitarian societies, when conditions allow, with resources becoming differentially economically defensible and transmissible, such individuals are well-poised to assume more permanent positions of leadership and to exploit initial advantages in resource distributions to gain greater wealth or power. Given that prestige-based forms of leadership are more common than dominance-based ones both within and across human societies, prestige and mutualism may be the major means by which egalitarian societies initially make the transition to unequal societies. Yet systems of dominance and coercion are by no means rare in human history or the modern world, suggesting that initial footholds based on prestige and mutualism may be converted to dominance and coercion-based inequality in situations entailing decreasing alternative options for subordinate individuals.[64]

Cultural Group Selection

Leaders emerge and are tolerated when the benefit they provide is greater than the associated cost to other individuals in the group. Coordination of large groups or complex tasks such as warfare present arenas in which leadership has been hypothesized to be valuable.[65,82,91] Yet such tasks are often transient in prestate societies, leaving open the question of whether and how task-specific roles persist and generate social inequality.

By linking behaviors at the individual and group levels, cultural group selection (CGS) may provide some preliminary answers. CGS proposes that social learning processes such as conformist learning can foster within-group similarity alongside between-group differences in norms and institutions, creating opportunities for differential group success.[92] Although most CGS models rely on low within-group differentiation, Henrich and Boyd[9] have shown that differentiation within groups, in conjunction with prestige-biased learning mechanisms, can lead to higher payoffs than more egalitarian group structures. More recently, Markowsky and Smaldino[93] have shown that within-group stratification in which a

group's most selfish members act as its leaders can promote success in conflicts with other groups. Using agent-based models predicated on well-known economic games (the Prisoner's Dilemma and Hawk-Dove) and in which group-level decisions are weighted toward the wealthiest individuals, they show that the selfishness that promotes acquisition of resources within groups facilitates success in intergroup conflict when leaders are at the helm of an otherwise democratic populace. (See Gavrilets and Fortunato[94] for theoretical arguments that selection can favor self-sacrificing leadership in intergroup conflict).

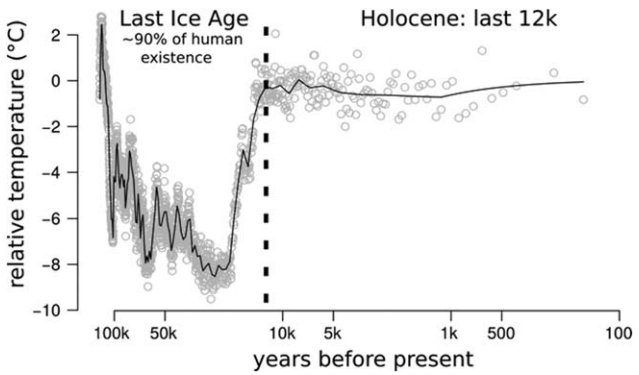

Figure 1. Data indicate a dramatic shift from the highly variable climate of the Pleistocene to much more stable climate patterns in the Holocene, beginning approximately 12,000 years ago. The temperature data shown are inferred from Antarctic ice-core oxygen-18 isotopes (adapted from Petit and collegues[131]).

Although few CGS models have been applied to understanding the evolution of PII per se, Markowsky and Smaldino's model demonstrates its potential usefulness in depicting processes that act across levels of organization in human societies. Agent-based simulations, while involving many simplifying assumptions, nonetheless provide clear predictions that can be empirically tested using economic games or ethnographic methods. Given that CGS models are consistent with both ecological explanations such as sedentism and climate change and individual strategizing with respect to resource allocation, they may prove to be useful in understanding the evolution of PII. Their relevance to explaining the emergence and spread of highly stratified systems is even clearer.[95]

WHY DOES INSTITUTIONALIZED INEQUALITY ARISE SO LATE?

Although our species has been cognitively modern for at least 100,000 years and possibly twice that long,[96,97] there is little evidence of inequality before the Holocene. There are a few tantalizing examples of possible inequality in the late Pleistocene; also, many potentially illustrative archeological sites have likely been drowned by rising sea levels. However, unambiguous evidence of institutionalized inequality arises only about 10-12,000 years ago.[5,98] This implies a long period during which our species maintained egalitarian systems. Why institutionalized inequality emerged so late is a key issue for understanding systems of inequality. Convincing explanations of PII must account for or at least be consistent with this late emergence.

Population pressure models have been cited to suggest that human habitats were not saturated until the Holocene, at which point PII arose as a solution to the problems of managing relatively dense populations.[4,19] However, population growth rates, even modest ones ($\geq$1%), lead to saturation much more rapidly (that is, in a few centuries) than envisioned in these arguments.[56] This suggests that even in the highly variable climate of the

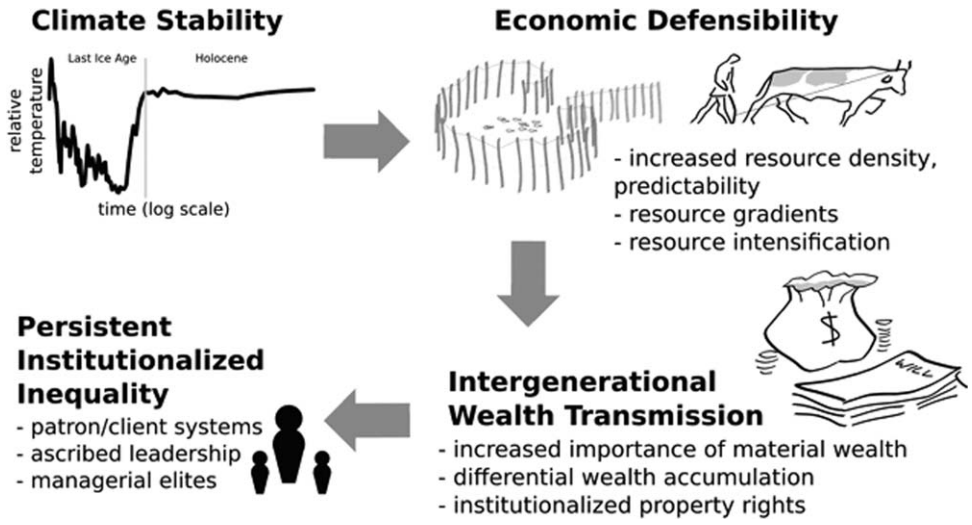

Figure 2. The climate stability shown in Figure 1 is a precondition for PII that arises in different times and places beginning in the Holocene. The main drivers of the emergence of PII in a given locale are ED (illustrated here by a fishing weir and agriculture) and intergenerational wealth transmission (particularly material wealth) supported by norms governing property and transmission rights.

Pleistocene, saturation would likely have occurred many times in periods of relatively stable, favorable climate, long before PII emerged.[99] This strongly implies that population pressure is not a sufficient cause of PII.

A related but distinct hypothesis is that population size, with the resulting density of social networks, generates complex cumulative culture, including PII. One version of this highlights scalar stress[100] as groups grow larger, with exponential increases in interaction rates, including conflict. Although larger groups do indeed have more potential for conflict, it is not clear why increases in population density should necessarily produce larger groups rather than larger numbers of groups through fissioning. Another potential role of population size hinges on the argument that cultural innovations are more easily generated and maintained in larger populations, with fewer innovations lost to drift.[101–103] Since PII is based on complex cultural institutions, it could be that only large populations can generate and maintain PII. However, the empirical evidence of widespread general associations between population size and cultural complexity is subject to debate.[70,104] In any case, cultural complexity is not identical to PII. Again, we note the absence of clear evolutionary mechanisms for producing PII in this scenario.

Many have suggested that environmental changes at the end of the Pleistocene were critical in fostering PII. Decline or extinction of large game, for example, may have encouraged forager societies to rely more heavily on resources such as wild grains and seeds,[105] which could later be subject to intensification, storage, and surplus production.[106] This resource intensification involved investment in facilities such as weirs and storage, as well as cultigens and domesticated animals; it was key to the accumulation of certain forms of material wealth, including territorial claims (property rights). We argue that such claims are critical to the emergence of social inequality.

A possible root cause of these changes is the dramatic decrease in climate variability following the transition from Pleistocene to Holocene conditions (Fig. 1).[107] Richerson, Boyd, and Bettinger[56] have argued that the Holocene shift to a relatively stable climate was a necessary condition for the emergence of agriculture. We generalize this, noting that although foraging economies persisted in many places throughout the Holocene, most exhibited decreasing mobility, resource diversification, intensification[108] and, in some cases, emergent PII.

The widespread ecological shifts associated with the onset of Holocene climates could thus explain why systems of PII were not sustainable in the Pleistocene. Specifically, high-frequency, high-amplitude climate fluctuations and resulting resource instability favored strong norms of resource sharing to mitigate risk,[109] as well as high mobility, which prevented the accumulation of resources[7] and the imposition of durable private-property claims.[55] The dramatic decline in climate variability around 12,000 years ago brought fairly rapid development of sedentism and differential control of both resource patches and stored surpluses in areas with sufficient resource potential. These changes presumably superseded leveling mechanisms associated with the redistribution of unpredictably acquired resources in hunter-gatherer groups, resulting in the potential for unequal accumulation of wealth,[7] as well as forms of resource intensification and human-resource coevolution that produced domesticates.[106] Of course in ecologies with lower opportunities for resource intensification and fewer economically defensible resources, some even relying on domesticates, egalitarian systems could and did persist.[22] Furthermore, the evolutionary perspective we advocate can also account for "reversals,"[15] or declines in inequality driven by reduced heterogeneity in control of resource patches or transmissible wealth. Notable examples of such reversals include the loss of hereditary inequality among Plains Indian groups that shifted from village-based horticultural systems with wealth-based hierarchies to nomadic equestrian bison-hunting, with leadership based on achievements in hunting and raiding.[110]

We conclude that PII emerges when and where it does because the predictability of resources brought about by Holocene climate stability, if coupled with sufficient resource patchiness or steep resource gradients (circumscription), is able to supersede leveling mechanisms in egalitarian societies.

CONCLUSIONS AND PROSPECTS

It is widely agreed that the evolution of PII from a relatively egalitarian starting point was a major transition in human social organization. The available archeological evidence indicates that PII arose relatively late (primarily or exclusively within the last twelve millennia) in our history as a species, then spread over most of the globe. This spread was sometimes a matter of independent local developments but, in other cases, involved diffusion, conquest, or displacement (even genocide). We have focused here on the former, emergent phases of the evolution of PII rather than the development of large-scale, stratified (class- or caste-based) multi-level systems (states or empires) or their direct effects on inequality in previously egalitarian societies. Prestige competition and mutualism are likely to

have driven the initial evolution of PII, but coercion and dominance eventually fuel increasing inequality, particularly when subordinates have few alternatives.

We have sought to identify the factors that best explain the emergence of PII. Although the climate stability characteristic of the Holocene appears to be a necessary condition for this emergence, it is certainly not sufficient, as shown by the persistence of egalitarian systems in various locales and periods throughout the Holocene. We contend that economically defensible (monopolizable) natural resources and transmissible (particularly material) wealth have been the key variables favoring the emergence of PII (Fig. 2), with institutional change and technological development supporting it. We conclude that PII emerges when and where it does because the predictability of resources brought about by Holocene climate stability, if coupled with sufficient resource patchiness or steep resource gradients (circumscription), is able to supersede leveling mechanisms in egalitarian societies. Limited status hierarchies among egalitarian foragers suggest that even in these societies, some individuals have traits that enhance their dominance or prestige.[18] When resources or new forms of wealth can be monopolized, such individuals (and their kin and allies) are poised to assert differential control of resources and use these over time to assume more permanent positions of leadership and economic advantage. However, this process is affected by existing norms and institutions and may also motivate the cultural evolution of new ones that instantiate private ownership and other aspects of PII.[5,55]

We hope we have demonstrated that an evolutionary framework helps to clarify and integrate perspectives that typically divide theorists on inequality. Further understanding of the evolution of inequality will require integration of research on multiple levels, including geospatial, temporal, population-specific, and individual. While all are fundamentally important to understanding the emergence of PII, the most critical empirical gaps involve addressing the emergence of inequality at the level of the individual operating within local social contexts. Market transitions in contemporary populations on the periphery of high-density, stratified societies are often accompanied by the development of inequalities in previously egalitarian societies, whether as a result of their assimilation into stratified systems or inherent properties of novel (typically material) forms of wealth associated with market transition. Such circumstances present an opportunity to study the emergence of inequality *in situ*, gaining an observational perspective we will never have on the prehistoric emergence of institutionalized inequality in human history (see Bettinger[111] for examples in archeology). There is no doubt of the timeliness of such research. The transition to increasing engagement with market economies is occurring globally, with profound implications for people's livelihoods, social relationships, and health.

This suggests that one of the highest priorities in research on inequality is to examine its emergence in the context of market transition in both ethnographic and archeological settings conducive to such analyses. Ideally, such studies will be comparative and include both broad definitions of wealth[44] and a variety of different methodologies. In ethnographic studies, this could include not just information on material wealth, but also biomarker and anthropometric assessments of health and embodied capital. Collecting multiple types of data will help elucidate how multiple forms of wealth interact to generate inequality. Likewise, longitudinal or panel data will allow us to elucidate the processes by which inequality emerges. Archeological studies should emphasize collection of multiple types of evidence for economically defensible resources and/or market exchange alongside evidence of inequality. Changes in patterns of resource access or use, exchange patterns, or markers of inequality through space and time will be especially informative. Whether ethnographic or archeological, such empirical studies will be most useful when they test theoretically based predictions and incorporate modeling[65,66,91] or cross-cultural comparisons.[44]

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