The ecology of inequality in animal societies

Eli D. Strauss[1,2,3,4], Daizaburo Shizuka[3]

[1]Department of Collective Behavior, Max Planck Institute of Animal Behavior, Konstanz, Germany

[2]Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, Germany

[3]School of Biological Sciences, University of Nebraska Lincoln, Lincoln, NE

[4]BEACON Center for the Study of Evolution in Action, Michigan State University, Lansing, MI

Corresponding author: Eli Strauss estrauss@ab.mpg.de

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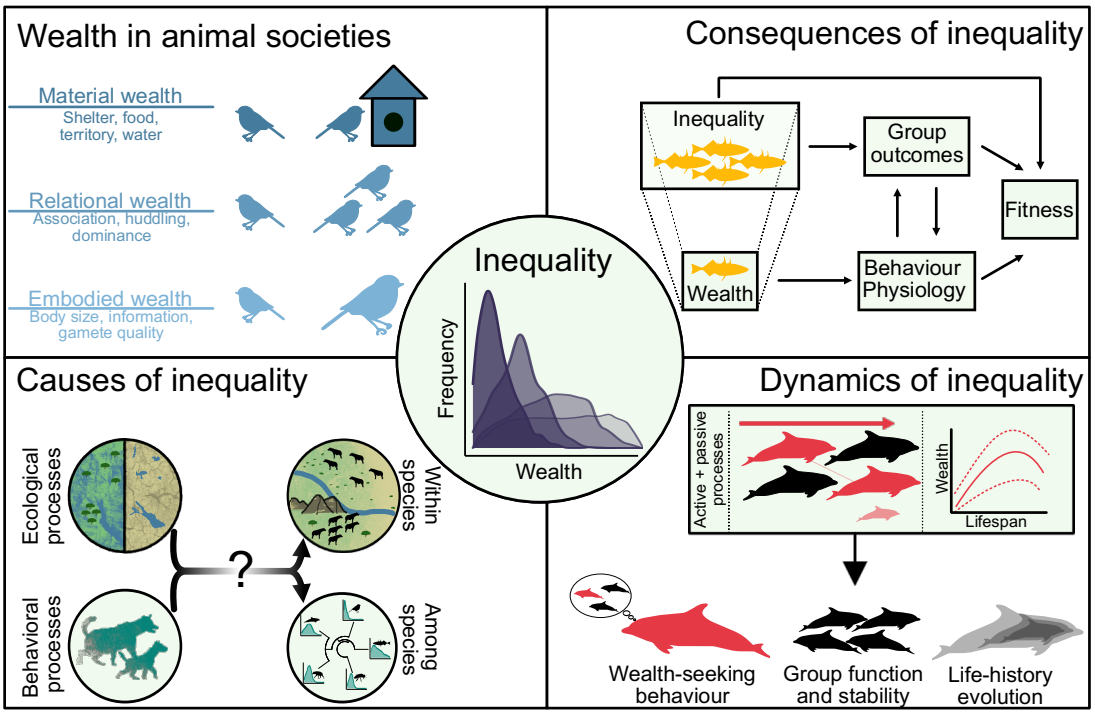
Abstract

Individuals vary in their access to resources, social connections, and phenotypic traits, and a central goal of behavioral ecology is to understand how this variation influences reproductive success and longevity. Parallel research on human societies has focused on the causes and consequences of variation in material possessions, opportunity, and health among individuals. At the core in both fields of study is that unequal distribution of benefits is an important component of social structure, but an explicit study of inequality is largely missing from evolutionary biology and ecology. Here we advance a research framework and agenda for studying inequality within an ecological and evolutionary context, drawing upon work in the human-oriented literature where applicable. We present four broad arguments for the ecological study of inequality: (1) wealth and inequality are taxonomically broad features of societies, (2) feedback loops link inequality to individual and societal outcomes, (3) very little is known about what makes some societies more unequal than others, and (4) inequality is dynamic, and these dynamics are relevant for social evolution. We hope that this framework will motivate a cohesive interdisciplinary approach to understanding inequality as a widespread and diverse biological phenomenon.

1. Introduction

Inequality is a general feature of human and non-human animal societies. Most species exhibit disparity among individuals' access to resources, physical condition, and the ability to coerce and socially connect with others. Sources of these disparities can be conceptualized as dimensions of *wealth*, and differences among individuals in these dimensions translate into differences in health, longevity, and reproductive success, ultimately influencing variation in fitness. Therefore, inequality takes many shapes and runs along multiple dimensions. Like other aspects of social structure, inequality is part of an individual-to-society feedback loop where individuals both shape and are shaped by their societies [1]. Human-oriented scholars have long grappled with the causes, consequences and dynamics of social inequality for individual well-being and the structure and function of societies [2], but an explicit study of these same topics is largely missing from evolutionary biology and ecology. We suggest that concepts of wealth, inequality and social mobility may also be important in explaining variation in the structure, dynamics, and evolution of animal societies.

Here we argue for a research agenda for studying inequality within an ecological and evolutionary context. This 'ecology of inequality' synthesizes concepts, questions, and empirical insights from the study of inequality in humans to investigate the ecological and evolutionary implications of inequality in human and non-human societies. We present four broad arguments for the ecological study of inequality: (1) wealth and inequality are taxonomically broad features of societies, (2) feedback loops link inequality to individual and societal outcomes, (3) very little is known about what makes some societies more unequal than others, and (4) inequality is dynamic, and these dynamics are relevant for social evolution. Under each section we review existing work and highlight areas requiring additional empirical and theoretical attention. We aim to motivate a cohesive interdisciplinary approach to understanding inequality as a widespread and diverse biological phenomenon.



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41 **Figure 1**. A schematic of the ecology of inequality. [center circle] Inequality describes the
42 distribution of wealth among individuals. [top left] Wealth is taxonomically broad and occurs in many
43 currencies, grouped into three aspects. [top right] Inequality emerges from individual wealth through
44 bottom-up causation and has top-down influence on individual outcomes, both directly and via its
45 effects on group outcomes. These effects are independent of effects of wealth. [bottom left] Multiple
46 ecological (e.g., food/water distribution) and behavioral (e.g., wealth inheritance) processes are
47 hypothesized to influence the amount of inequality in societies, but it's not clear at what scale this
48 influence occurs or to what degree these processes operate across species. [bottom right] Inequality is
49 dynamic. Active and passive processes produce changes in wealth within an individual's lifetime and
50 across generations, leading to typical wealth trajectories over the lifespan. The amount, timing, and
51 direction of wealth trajectories are expected to exert selection on individuals to optimize their
52 experienced costs and benefits of sociality.

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2. What is wealth and inequality in animal societies?

Non-humans don't have bank accounts, so how can they be wealthy? Economists and evolutionary anthropologists have long known that wealth can take many forms [3]. Rather than consisting only of money, wealth manifests in many *currencies*, or quantities of attributes or possessions that impact an individual's access to "valued goods and services" [4]. Although the currencies of wealth are numerous, they can be pooled into three superseding categories (here '*aspects';* Figure 1, upper left) [4–6]. *Material wealth* denotes extrasomatic currencies such as money, land, or livestock. *Relational wealth* is comprised of social connections, often measured as ties in a network of relevant social interactions or relationships such as food sharing, prestige, or hunting. Finally, *embodied wealth* refers to attributes of individuals, such as size, strength, or knowledge. This framework has been applied to a dataset of diverse human societies to reveal how the relevance of different aspects of wealth vary across societies, how some aspects of wealth are more readily transmissible across generations than others, and influences on the severity of inequality across societies [6–8].

This framework reveals how animal societies are also structured by multidimensional wealth. These same three aspects – material, relational, and embodied wealth – map clearly onto established concepts in ecology and evolution, like constructed/defended niches, social niches, and phenotypic traits. Embodied wealth is made up of phenotypic currencies such as fat reserves, sperm quality, or information. Classic examples of embodied wealth are condition-dependent signals, like the male house-finch's (*Carpodacus mexicanus*) bright red plumage [9]. Material wealth currencies include defendable resources such as food items, nest sites, water sources, and territories, as well as 'constructed' resources such as food caches, shelters, and nest decorations [10]. For instance, material wealth is prominent in acorn woodpeckers (*Melanerpes formicivorus*), who invest heavily in both granary construction (the work of generations of woodpeckers) and in the collection and storage of acorns within the granary [11]. Finally, relational wealth describes an individual's social niche [12], encompassing social relationships such as association, grooming, food sharing, huddling, or dominance. Considerable evidence points to the impact relational wealth has in animal societies [13–15] – for example, social alliances in spotted hyenas (*Crocuta crocuta*) influence social rank and,

consequently, fitness [16]. There is broad consensus in evolutionary theory that material and relational wealth (i.e., constructed and social niches) can influence fitness, drive adaptation, and contribute to evolutionary change [17]. Existing biological concepts also describe the transmission of wealth across generations via mechanisms of genetic and epigenetic inheritance, ecological inheritance [18], and social inheritance [19]. Therefore, much existing work in ecology and evolution has in fact already demonstrated the importance of wealth in non-human societies.

Inequality describes the spread and skewness in the distribution of wealth (Figure 1, center circle). In humans, wealth distributions are frequently broad, heavy-tailed distributions such as lognormal, exponential, or power-laws (or their combination) [20,21]; operational measures of inequality are designed to capture features of the spread and skew of these distributions (Box 1). The few studies that have examined inequality *per se* in non-human systems have found distributions of wealth similar to that of humans [22–24]. Further, research topics in behavioral ecology such as leadership [25], reproductive skew [26], and dominance [27] are fundamentally concerned with the role of inequality in structuring societies. Thus, although the explicit study of inequality in ecology and evolution is missing, there is considerable evidence supporting the argument that wealth and inequality are taxonomically broad features of societies.

Box 1

Here we provide a brief introduction to the methods for measuring inequality, intended to introduce the reader to what is an extensive body of literature in economics. Distributions can differ from pure equality in numerous ways [20,28–30]. When empirical wealth distributions are well-described by the functional form of one or more distributions, inequality can be described analytically via the parameters specifying the distribution [21]. Alternatively, inequality can be measured by summarizing the amount of wealth held by a individuals in a certain quantile (e.g., the proportion of total wealth held by the wealthiest 10% [31]) or by comparing the wealth of individuals in different quantiles (e.g., the ratio of wealth held by the top 20% to wealth held by the bottom 20%). Finally, "index" approaches summarize inequality into a single numerical index. The Gini index is the most commonly used metric of inequality, and although most often applied to income, it has also been used to study

inequality in distributions of monetary wealth in WEIRD societies [32], land ownership [8], social connections, faculty production by different universities [33], body size [6], reproductive success [34], plant sizes [35], and hermit crab (*Pagurus longicarpus*) shell sizes [23]. Because a single parameter cannot fully summarize the shape of a distribution, different indices are sensitive to different features of unequal distributions [20]. Thus, it is wise to use multiple measures to gain the clearest picture of inequality and to avoid identifying patterns that are detectable only by one method. Finally, it is important to note that most of these methods were developed to describe inequality in large nation-states, and methodological challenges remain to facilitate comparative approaches to inequality in smaller societies such as those found in non-human systems [28,29,36].

3. What are the consequences of inequality?

Inequality has top-down effects on individual fitness that are not detectable by examining wealth at the individual level alone. Furthermore, inequality can influence outcomes for individuals directly or by impacting group outcomes (Figure 1, upper right). Although there have been many studies in humans demonstrating this influence of inequality on individual and societal outcomes [37–39], very little work in non-humans has explored pathways by which inequality impacts individuals, societies and evolution.

Inequality impacts individual health and well-being [15,39–41]. In humans, more unequal societies are often associated with negative individual and societal outcomes [37,38]. An evolutionary comparison across primates, including humans, revealed that life-expectancy increased with life-span equality, further indicating that inequality covaries with individual outcomes [42]. Inequality-induced chronic psychosocial stress, or "status anxiety" [43] is a proposed mechanism by which inequality might impact individual health and well-being. Status-induced stress can affect both low- and high-wealth individuals. In humans, status anxiety is more extreme in societies that are more unequal, even for individuals of high social status [44]. However, low-wealth individuals face larger stress burdens than wealthy individuals, either by experiencing more stressors or by experiencing more severe effects of stressors [45,46]. In an experimental study of the effects of psychosocial stress on longevity, subordinate lab rats showed reduced health and survival compared with dominants when housed in

cages that allowed for sensory exchange but no physical contact [47]. Overall, widespread association between measures of wealth and individual outcomes supports the broad hypothesis that social gradients are a "fundamental cause" of differences in health outcomes [15,48].

Individuals attend to inequality within their societies and alter their behaviors accordingly. Experiments in primates, corvids, and domestic dogs suggest that the perceived value of a resource is influenced by an individual's observations of the value of the resources their group-mates receive [49–52]. Individuals often then alter their social behavior, for example by punishing individuals who receive the higher-valued resource [53]. In humans, an individual's wealth influences their perceptions about the degree of inequality in society [54] and their status-seeking behaviour [55]. In many species, individuals use social information when making decisions about how and with whom to compete [56,57]. In sum, intra-group competition and inequality are linked by a feedback loop involving individual perception of their own social status, the social status of others, and the amount of inequality in the group. To understand this feedback loop, more work is needed to explore how individuals perceive social structure and inequality within their groups. Systems where signals of wealth can be manipulated independent of actual wealth provide a means to experimentally manipulate the perception of inequality.

Inequality can influence group outcomes by altering the benefits individuals gain by investing in the success of the group or by influencing the ability for groups to achieve collective action. Reproductive skew theory [26,58,59] suggests that inequality in reproduction leads individuals to experience divergent benefits of group living, and consequently, divergent motivation to preserve the productivity or persistence of the group [60,61]. Inequality can also influence a group's ability to cooperate or achieve collective action. In cooperation experiments with chimpanzees, bonobos, and cottontop tamarins, evidence suggests that species that divide the rewards of cooperation more equally are more likely to show cooperative behavior [62,63]. Theoretical and empirical studies of collective action problems (e.g., public goods game) suggest that inequality has complex and often unpredictable effects on cooperative behavior [64–72]. However, a rough pattern emerges in the literature suggesting that the effect of inequality on cooperation might depend on the type of wealth

under consideration. In studies where individuals vary in the resources they can invest in cooperation (i.e., material wealth), inequality typically reduces cooperation [64,65,72]. However, inequality in social influence can promote cooperation by eliminating free-riders and overcoming coordination challenges [66,70,73–75]. Other evidence suggests that inequality can influence group outcomes by improving or impeding the function of groups, for instance by altering costs of coordination, resilience to variable environmental conditions, or ability to compete with other groups [70,74,76,77]. Overall, the complex results from theoretical studies suggest a need for empirical work on the links between inequality, individual outcomes, and group function in animal systems.

Importantly, the hypothesized effects of inequality we discuss here operate in addition to any direct effects of wealth. For example, low-wealth individuals might suffer costs associated with shortage, but additionally experience status anxiety, attend and respond to the distribution of wealth in their society, and engage in increased or decreased cooperation with their group-mates. As a result, multiple causal pathways link wealth and inequality to individual fitness (Figure 1, upper right). While evolutionary theory primarily focuses on the direct effects of (typically embodied) wealth on variation in fitness, a broader exploration of the top-down effects of inequality on individual and group outcomes will help unravel evolution dynamics that arise from living in societies.

Why are societies unequal?

Multiple behavioral and ecological processes have been hypothesized to influence the amount of inequality within societies, but tests of these hypotheses are rare. In particular, it is especially unclear to what extent these hypothesized mechanisms might explain variation within vs. among species (Figure 1, lower left). Thus, understanding the forces that produce inequality requires two primary steps: 1) characterize variation in inequality within and among species, and 2) test hypothesized mechanisms influencing inequality.

Some aspects of inequality seem to be relatively flexible, whereas others are more constrained. For example, in a population of olive baboons (*Papio anubis*) in Kenya, a mass-mortality event prompted a long-term shift towards a more tolerant society with more equally distributed stress burdens, perhaps

189 as a result of the death of the individuals who competed most intensely for high status [78]. However,
190 a comparative network motif analysis of dominance hierarchies suggests strong constraints on their
191 structure related to transitivity of dominance relations [79]. Furthermore, phylogenetic constraints
192 may limit within-species plasticity in inequality. In macaques, a suite of behaviors related to
193 inequality in within-group conflict covary across species, producing macaque societies with different
194 'social styles' and suggesting potential phylogenetic constraints on social structure [80,81]. More
195 longitudinal and phylogenetic studies will be crucial to advance our understanding of plasticity and
196 constraint in inequality across species.

197 What behavioral and ecological mechanisms influence variation in inequality within and among
198 species? Ecological conditions have long been hypothesized as a driver of inequality in access to
199 resources [82,83]. The patchiness of resource distribution [83–85], resource intensification [86], and
200 the defensibility of resources [87] have been proposed as hypothesized ecological mechanisms
201 influencing inequality (but see [84,88]). Additionally, inequality may be influenced by individual
202 behavioral traits such as leveling coalitions used to control would-be dominants [89], aversion to
203 unequal payoffs [49], preferences regarding perceived inequality [90], status seeking behavior [91],
204 visibility of wealth [92], and cognitive processes relating to social competition [56]. Finally, self-
205 reinforcing dynamics – where "rich-get-richer" feedbacks lead wealthy individuals to gain more
206 wealth – can also influence the amount of inequality in societies [93,94] (see also section 5).

207 Although drivers of inequality may differ among species or wealth aspects, some hypothesized causes
208 of inequality are expected to operate across contexts. For example, the social transfer of wealth is one
209 hypothesized driver of inequality that is likely to operate widely [6,95]. In a broad survey of human
210 societies with diverse production systems, increased fidelity of transmission of wealth across
211 generations was associated with more extreme inequality [4,6]. Although to date this hypothesis has
212 only been investigated in humans, the behavioral inheritance of, for example, territory [96],
213 knowledge [97,98], social relationships [19], and food caches [100] provide ample contexts in which
214 to test this hypothesis in diverse systems. For instance, the social inheritance of dominance status in
215 spotted hyenas and old-world primates may drive inequality in dominance among lineages [16,99]. In

fact, the widespread transmission of wealth across generations points to the evolutionary importance of non-genetic inheritance (e.g., [18]) and selection in response to multigenerational processes [101]. Another broadly-operating hypothesized driver of inequality is intergroup conflict. When unequal groups are more effective or willing competitors, selection for success in intergroup conflicts can lead to increased within-group inequality [73,77,102,103]. Here there is potential for positive feedback when the individuals who benefit most from intergroup conflict are also effective initiators of these conflicts, as seen in humans and banded mongoose (*Mungos mungo*) [104,105]. Finally, environmental stressors arising from climate change are expected to impact many species, highlighting another potentially broadly-acting driver of inequality that we need to better understand. Studying shared processes influencing inequality in diverse wealth currencies and species is key to understanding the evolution of inequality and its role in societies.

4. How does inequality change over time?

The study of the dynamics of inequality provides a powerful lens through which to gain new insight about individual outcomes, long-run structures in inequality, and the stability and persistence of groups over time. One avenue for understanding these dynamics is through *social mobility*, a suite of concepts borrowed from economics that describe the dynamics of wealth measured at the individual or lineage level. Aggregating these measures across members of a social group reveals the society-level tendency for individuals or lineages to gain or lose wealth over time, producing more rigid or fluid societies.

Social mobility can vary in the time-scale at which it is assessed and the processes by which it arises. Intra- and intergenerational mobility classify the generational scale at which mobility occurs. *Intragenerational mobility* describes the degree to which individual wealth changes, producing wealth trajectories over the lifespan. *Intergenerational mobility* refers to the change in wealth within lineages across generations, and is the type of social mobility most often studied in humans [6,106–109]. Examining the correlation between parents and offspring wealth provides an empirical measure of the extent to which an individual's position in society is malleable versus predetermined by the conditions into which they are born [110]. Increasingly, researchers are expanding the study of intergenerational

mobility to include multigenerational effects, such as the effects of grandparents or other more distant kin [111,112].

In addition to the generational scale at which mobility occurs, it is also important to distinguish the processes that produce mobility and the rate at which mobility occurs. Processes influencing social mobility can be active or passive: *active mobility* occurs when an individual's wealth changes with respect to their groupmates by reversing the wealth-ordering of individuals, whereas *passive mobility* occurs as a result of demographic processes [113]. Social mobility resulting from active and passive processes can occur gradually or precipitously. Demographic processes like births and deaths frequently produce gradual changes that have direct and indirect effects on social structure by removing and replacing individuals and altering existing social relationships [114]. In some cases, large demographic changes can push societies over tipping points, or precipitous shifts in social structure that can show hysteresis [115]. Revolutions [116], mass mortality [78,116–118], group fissions [119], the arrival or loss of certain individuals [120–123] and expulsions of lineages [124], are examples of active and passive processes that could produce precipitous changes.

The long-term additive combination of social mobility produce *long-run inequality*, which describes equilibrium patterns of inequality around which a given society fluctuates [24,31], assuming such an equilibrium state exists. Long-term perspectives are crucial for probing the possibility that societies or species tend towards an equilibrium quantity of inequality and social mobility. Understanding where a society sits relative to its expected equilibrium state creates opportunities for exploring the forces that lead societies to deviate from or return to their equilibria. Taking this long-run perspective also enables understanding of societies with distinctively low social mobility. This is known as 'durable' inequality [125], or inequality that persists across individuals, time, or generations [87]. Durable inequality can give rise to social classes, where individuals of different classes form social networks with different structures, face different mortality sources, and cope differently with stressful conditions [126–128]. One process producing durable inequality is self-reinforcing dynamics, where already wealthy individuals accrue disproportionately greater wealth, [22,94,129–131]. Preferential attachment and "rich-club effect" models of social relationships demonstrate how

relational wealth can show such self-reinforcing dynamics [132,133]. Frequency-dependent or fluctuating selection may be a counterforce that inhibits the buildup of durable inequality by altering fitness landscapes [134].

Patterns of social mobility may influence evolution of a wide suite behavioral strategies such as tolerance and wealth-seeking behaviour, as well as life-history traits related to pace-of life (Figure 1, lower right). In species in which wealth increases with age through passive processes, selection should favor traits associated with conflict avoidance, tolerance, and slow pace-of-life, which would allow for individuals to avoid the costs of escalated competition and still enjoy the benefits of elevated wealth. In contrast, societies in which wealth declines with age should select for early reproduction and a faster pace-of-life. Where upward intragenerational mobility is achieved through active processes, selection is expected to favor individuals who challenge their groupmates, behave 'politically,' and have a faster pace-of-life. Low intergenerational mobility is expected to amplify selection on traits related to intragenerational mobility, as any changes within a generation are likely to persist and influence future generations. This hypothesized selection driven by social mobility reflects ways in which patterns in the dynamics of social structure can feed back to influence the evolution of individual traits [1].

Contrasting hypotheses about the influence of social mobility on the stability of social groups highlights potential tradeoffs in the evolution of social structure. On the one hand, some have suggested that upward social mobility is crucial for long-term group stability, as individuals are expected to leave societies where they have no opportunity for advancement or wealth acquisition [24]. This pattern of upward mobility is prominent in societies where individuals 'queue' for wealth, such as in long-tailed manakins (*Chiroxiphia linearis*) [135], where individuals move up the queue through passive processes (e.g., death of wealthier individuals) [24,135–137]. In contrast, overly frequent active mobility can cause social instability, which is associated with negative consequences for individuals and societies [41,120,138,139]. This suggests the potential for stabilizing selection favoring societies with intermediate levels of social mobility. These contrasting perspectives emphasize the need for theoretical and empirical work that generates and tests hypotheses about the

297 link between social mobility and the functioning of societies in diverse species. A primary aim should
298 be to develop quantitative models of divergent and of unifying principles underlying dynamics of
299 social inequality and social structure across species, similar to the recently developed study of
300 'cliodynamics' in human societies [140].

301 **5. Conclusions and future directions**

302 A key question in ecology and evolution is how the structure of groups arise and impact the
303 individuals that comprise them [1]. Inequality in the distribution of wealth – be it relational, material,
304 or embodied – is a group-level feature that is hypothesized to impact individual and group outcomes.
305 Despite an intense interest in the origin and impacts of inequality in human societies, inequality in
306 animal societies is only investigated in isolated contexts (e.g., dominance, reproductive skew,
307 leadership) and remains disjointed from the study of inequality in economics, anthropology,
308 sociology, and psychology. Here we coalesce these disparate studies of inequality in biological
309 systems into a framework that allows for the study of inequality across ecological and evolutionary
310 contexts. Where possible, we take steps to align this biological approach with work in the human-
311 oriented literature. Throughout the framework, we balance the aim of identifying common principles
312 underlying the causes and consequences of inequality with the reality that inequality may operate
313 uniquely in different species and contexts.

314 Three broad ongoing questions characterize the study of wealth and inequality. First, it is crucial to
315 understand how inequality impacts individuals. By definition, having more wealth is better than
316 having less, but the key here is to explore how the distribution of wealth impacts individuals
317 independent of direct effects of wealth. Evidence suggests that individuals attend to the amount of
318 inequality within their societies, and that inequality may itself have adverse effects for individuals and
319 mixed effects for the function of societies. Here, theoretical work has outpaced empirical work –
320 which has focused primarily on humans – so a primary goal should be to examine the impacts of
321 inequality on individual and group outcomes in non-human systems. Experimental studies of
322 inequality in lab populations is a promising tool for disentangling the effects of inequality from the
323 effects of wealth *per se*. Finally, an ongoing surge in work on the mechanisms underlying social

gradients in individual outcomes will continue to shed light on potential avenues by which inequality influences fitness [15].

A second broad aim of the ecology of inequality is to understand the forces that cause inequality, both in the short term and at evolutionary time-scales. Evidence from dominance hierarchies has demonstrated that some aspects of inequality can be plastic – even sensitive to the behavior of a single individual – whereas other aspects of inequality are highly evolutionarily constrained. Phylogenetic analyses will be crucial for detecting evolutionary patterns in inequality. A long history of empirical and theoretical work highlights the important role of ecology in influencing inequality in access to resources, mating patterns, and intragroup/intergroup conflict. Biogeographical approaches may be useful here for identifying ecological correlates with inequality at a global scale. However, in addition to exogenous forces like ecological conditions, it is likely that self-organizational processes and feedback loops play a large role in influencing the nature of inequality in different societies. Self-organizational processes shared across species and types of wealth might explain why inequality is such a common feature of societies across the animal kingdom. Finally, dual inheritance models of gene/culture coevolution offer a promising framework for understanding feedback loops in structuring inequality and the processes that produce plasticity and constraint in inequality within and among species.

Third, it is crucial to take a dynamical perspective on inequality to understand selection on individual traits, long-term patterns in inequality, and the stability and persistence of groups. Social mobility – or changes in wealth – can occur due to various processes and at different times scales, leading to higher-order patterns in inequality among individuals and their descendants, such as social classes or family dynasties. However, very little is known about the existence or implications of these higher-order patterns in inequality in non-human systems. Long-term studies that track groups and their constituents over multiple generations are uniquely situated to address this knowledge gap. Furthermore, we call for theoretical models that explore how the behavioral processes producing social mobility and the generational-scale on which mobility occurs impact the evolution of life-history traits and wealth-seeking behavior. Lastly, the flip-side of mobility is instability, which

reflects a breakdown of the predictability of society, and can negatively impact groups and individuals. Conflicting predictions about the impact of social mobility vs. instability highlight a potential tradeoff between individual opportunity for social advancement and the need for social stability. Here, more theory is needed to generate hypotheses that can be tested in empirical systems.

Inequality is a curiously widespread feature of societies. The link between wealth – as broadly defined here – and fitness has been a central focus in evolutionary biology and behavioral ecology, but much less is known about the causes and consequences of the distributions of wealth. The framework presented here offers a way forward for exploring the causes of inequality, its impacts on individuals, and its role in social evolution. The framework is built upon a multidimensional concept of wealth, which allows inequality to be understood in specific contexts while also providing a means for comparative insight and the identification of general features of inequality operating across species. This approach at once strengthens biological and sociological fields by integrating perspectives and facilitating the exchange of ideas, paving the way for new insights into ecological and evolutionary forces impacting social organisms.

Author Contributions

Both authors contributed to all aspects of the manuscript.

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