Ecological Civilization

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Evolutionary and Economic Foundations for an Ecological Civilization

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ABSTRACT: Human civilization threatens the life support functions generated by global ecosystems. Humanity must forge an ecological civilization to avoid collapse. We apply evolutionary theory to the human system, with an emphasis on the economy, to understand how we have arrived at our current predicament and to suggest paths forward. Neoliberal economic theory claims that within markets, the self-interested behavior of individuals and firms maximizes societal welfare, while some strands of evolutionary theory claim that selfish individuals will outcompete their selfish conspecifics. Yet, cooperation is ubiquitous. Humans have become more interdependent than ever. We present a theoretical argument that the structure of the global economy is best explained by multilevel selection (MLS)—an evolutionary process wherein competitive individuals outcompete cooperative individuals within groups, while cooperative groups outperform competitive groups. MLS helps explain why both cooperation and selfishness co-exist, with cooperation the most adaptive social behavior at higher-scales. We conclude that achieving an ecological civilization will not only require cooperation at the global scale, but also the forging of a new relationship between humans and the rest of nature, akin to the relationship between a human cell and the human body.

Keywords: Social dilemmas; Cooperation; Altruism; Multilevel selection; Major evolutionary transitions; Cultural evolution; The global economy

1. Introduction

There is increasing recognition that the social and ecological costs of human civilization are so extensive that humanity's survival demands a new approach to civilization based on sound ecological principles. Humanity must collectively forge an ecological civilization or perish. Fortunately, the history of life on Earth suggests that this is not a quixotic quest doomed to failure. Rather, it requires continuation of the evolutionary processes that forged the continually evolving complex global ecosystems of which humans are but one component. The objective of this article is threefold: to explain (1) how these processes gave rise to both the global ecosystem and the human subsystem; (2) how the modern economy has come to undermine this process; and (3) what is required to build an ecological civilization on sound ecological, evolutionary, and economic foundations.

We begin with a focus on the global economy—an interconnected web of trading partnerships, financial transactions, and exchanges that has become more integrated and complex over time. It is also a subsystem of the interconnected web of plants, animals, water, air, and minerals that make up the global ecosystem. What are the underlying forces organizing the economy and driving its evolution?

According to the textbook neoliberal economic theory, the global economy is driven by the self-regarding, rational pursuit of utility and profit and organized by a price mechanism that rations selfish individuals' and firms' access to scarce resources [1]. Dated, but still influential, strands of sociobiology and neo-Darwinian theory use this same logic to argue that the global ecosystem is the result of the competition between individuals within a species and between species to maximize relative reproductive fitness and perpetuate their genes. In a world populated by these self-regarding, maximizing agents, competition ensures that a state of Pareto optimality is reached—a situation where resources cannot be reallocated to improve the wellbeing of any agent without making another agent worse off. Conversely, cooperation—which requires concession or delayed gratification for the benefit of others—is a suboptimal strategy.

If competition is the fundamental force behind the global economy—purported by neoliberal advocates to efficiently allocate resources to those best positioned to maximize welfare and thereby generate the most value—what role, if any, does cooperation play? We reject the contention that competition is an economic panacea and the driving force behind the global economy. Instead, we proclaim that human cooperation is robust across all societies [2] and just as crucial to the global economy as competition.

The presence of these dual forces presents a conundrum. If competition is the most efficient strategy that enables individuals to maximize their personal welfare—as textbook neoliberal economics contends—why is cooperation and self-sacrifice for the benefit of the group so widespread? How can these two forces persist side-by-side within the global economy, and how may their interaction shape its organization and evolution? In their 2006 paper, Traulsen and Nowak [3] passingly suggested that "an important organizing principle" for structuring "the economics of nations" could be the evolutionary process called "multilevel selection" (MLS)—a phenomena whereby competitive (selfish) individuals outcompete cooperative (altruistic) individuals within groups, but groups with a higher proportion of altruistic individuals outcompete groups dominated by selfish individuals. Natural selection can act on both the individual and the group. A corollary of this theory is that selfish individuals undermine the welfare of the group.

Though still controversial in the field of evolution, we believe the preponderance of evidence confirms that MLS has been important to the evolution of our complex global ecosystem [4]. Until now, the application of MLS to the global economy and the emergence of an ecological civilization remain unexplored. To address this gap, the present paper examines the application of MLS to the global economy and to the relationship between humanity and the rest of nature. Befitting our approach, we adopt the Polanyian definition of economics as how people interact with nature and each other to provision their material needs [5]. We hypothesize that cooperation persists because it is the most adaptive social behavior at higher scales, and achieving an ecological civilization requires scaling up cooperation between nations and between humanity and the rest of nature. In doing so, this paper advances three arguments.

First, the global economy functions as a complex, nested system of different interdependent entities, in which groups at one level of the nested system become individuals at the next. Like a matryoshka doll, the global economy ranges from individuals and local communities to firms, states, and the international community, another term for humanity. The outermost matryoshka doll, the global ecosystem, sustains and contains all the economic subsystems, yet remains neglected by most economic theories and systems. Second, this superstructure—which this paper dubs the socio-ecological hierarchy (SEH)—is conducive to MLS serving as an "important organizing principle" of the global economy and of human interactions with the rest of nature, helping balance cooperation and competition. Third, cultural—not genetic—variables, such as social norms, identities, institutions, and rituals, serve as vehicles for transmitting values that often help prioritize higher-level cooperation and subvert lower-level competition at various points along the

SEH. In this context, natural selection primarily operates not on genes, but on the relative economic performance of agents within and across the various levels of the SEH.

The forces of competition and cooperation "coexist in every known society—not only within groups, but also between groups, and not only among kin but also among non-kin" (p. 14) [6]. Social dilemmas, situations in which the group benefits from cooperation but the individual benefits in the short term from selfishness, regardless of what others do, favor group-level selection. Social dilemmas, ranging from grazing too many sheep on a shared pasture to global climate change, pervade the global economy at every level of the SEH. The ubiquity of social dilemmas throughout human history has favored cooperation at increasing scales, from small bands of hunter gatherers to countries with over a billion citizens, solidifying its role as the backbone of our species' success [7].

Section 2 of this article explains in greater detail the theory of multilevel selection. We maintain that MLS is important to human cooperation and suggest that, by operating on cultural systems, it serves as an organizing force behind the modern global economy. Section 3 examines individuals, communities, firms, states, humanity, and the global ecosystem through the lens of MLS and posits that an ecological civilization will require cooperation at the international scale, together with the forging of a new relationship between humanity and the rest of nature. Sections 4 and 5 provide a discussion and conclusions, respectively. By regulating the friction between competition and cooperation over time, MLS can favor agents who engage in selfish economic behavior at lower-scales but favor more altruistic groups that cooperatively manage resources at higher scales.

2. Methods: Multilevel Selection Theory as a Tool for Understanding the Prevalence of Cooperation

2.1. The Evolutionary Paradox of Human Cooperation

Game theory suggests that Human cooperation is an evolutionary puzzle due to its paradoxical benefit-to-cost structure. Every time two agents participate in a one-shot prisoner's dilemma game, a representative type of social dilemma, they face four possible combinations of choices: (1) both agents cooperate, (2) both agents compete, (3) one agent cooperates while the other competes, and (4) one agent competes while the other cooperates. Under these one-shot conditions, self-interested agents are mathematically incentivized to choose competition over cooperation because it is the most probabilistically safe default strategy. A cooperative act requires an agent to sacrifice their own material welfare—or forgo opportunities to enhance their own welfare—to benefit others. If both agents cooperate, absolute welfare is maximized. However, if one competes while the other cooperates, or vice versa, the competing agent can free ride, reaping the benefits of the transaction without reciprocating. This increases the competitive agent's relative success. When both agents compete, a stalemate is reached. This outcome—called a Nash equilibrium—is a theoretically stable and risk-averse state in which no agent can gain or lose an advantage over the other.

These game-theoretic dynamics became a central foundation for a now-dated, yet still influential, evolutionary framework known as sociobiology. Within this paradigm, individual organisms are assumed to be primarily concerned with their comparative fitness, generally disregarding others except when they are close genetic relatives. Although subsequent developments in evolutionary theory have expanded the scope for cooperation—recognizing, for instance, that competition may be suspended in cases of reciprocal altruism, tit-for-tat strategies, and repeated prisoner's dilemma interactions—the overarching framework treats the individual as the fundamental unit of the biological world [8]. In this formulation, cooperation is relevant only to the extent that it confers advantages to the individual, thereby maintaining the idea that organisms are principally motivated to competitively displace conspecifics—especially if they are unrelated. Dawkins [9] formalized this perspective in neo-Darwinian terms in *The Selfish Gene* (p. 20), where he poetically states: "They are in you and me; they created us, body and mind; and their preservation is the ultimate rationale for our existence. They have come a long way, those replicators. Now they go by the

name of genes, and we are their survival machines". This view of evolution as a metaphorical battleground for the "survival of the fittest" positions organisms—including humans—as subordinate to their unrelenting and selfish interests, largely dismissing cooperation as irrelevant unless it enhances their individual welfare.

This early strand of sociobiology bears close parallels to neoliberal economic theory, which itself drew ontological inspiration from warped interpretations of original Darwinian thought (Gowdy, 2004). Classic sociobiology asserts that the survival interests of organisms and their genes are primary. Similarly, neoliberal economic theory places central importance on the atomized interactions between individual consumers and firms. Just as the first principles of early sociobiology state that organisms are preprogrammed to reproduce, the core tenet of neoliberal economic theory is that agents possess an urge to consume and produce commodities endlessly. In both frameworks, fitness is the measure of success: for organisms, it is reproductive success, while for economic agents, it is income and profit maximization. Competition is posited as the optimal strategy for achieving these goals, as cooperation is seen to reduce the wellbeing of individual economic agents by limiting their ability to accumulate income and profit. In fact, this is a cornerstone of welfare economics, which posits that competitive markets generate a welfare maximizing equilibrium [10]. In sociobiological terms, the Nash equilibrium reflects a state where no organism can improve its welfare without reducing another's. Similarly, in neoliberal economic theory, Pareto optimality is reached when commodities cannot be redistributed without making someone else worse off. Consequently, any intervention—especially government action—that seeks to modify these behaviors is regarded as futile.

Above all, the neoliberal economic paradigm conceives the economy as a system composed of competitive individuals and firms motivated primarily by the pursuit of self-interested, subjective preferences—implicitly treating this motivation as an innate predisposition. In this view, competition is treated as an almost automatic response that aligns most naturally with decentralized market institutions, which are presumed to maximize total welfare understood as the aggregate sum of individual utility functions.

Despite cooperation theoretically being a drag on an individual's wellbeing, it is ubiquitous. Human beings are equipped with an evolved, species-specific set of cooperative habits, supported by a suite of physical and social mechanisms that manifest in intuitive prosocial decision-making and altruism [11]. Within laboratories, experiments show that people routinely cooperate and are willing to incur a cost to punish others they perceive as being unfair. In ultimatum games, one participant decides how to divide an endowment and makes an offer to another participant, who can accept or veto the proposal. If payoff-maximization governed behavior, proposers should offer the smallest possible amount, and responders should accept it. Research findings reveal that "a majority of proposers offer 40 to 50% of the total sum, and about half of all responders reject offers below 30%", implying that "players have preferences which do not depend solely on their own payoff" [12]. Even in one-shot anonymous ultimatum games, where participants cannot communicate or be influenced by non-verbal cues, proposers and responders frequently converge on splits of 30–70% and 50–50%. The evidence suggests fairness is favored in one-shot anonymous ultimatum games. Cooperation even prevails in one-shot prisoner's dilemmas, where defection goes unpunished. Numerous studies find that roughly three-quarters cooperate despite defection being the supposedly dominant strategy [13,14].

Outside of the laboratory, similar doubts are raised. One study of 15 different small-scale societies found that cooperation was widespread, with no evidence for the 'Economic Man' model in any culture [2]. An anthropological survey of 60 diverse and unique societies identified cooperation as a universal moral value [15]. Being other-regarding is perhaps a universal moral trait.

2.2. Human Evolution as a Major Evolutionary Transition

The portrayal of humans as independent, selfish agents is challenged by the fact that the biological world is, in large part, shaped by extensive and active cooperation. Around 2 billion years ago, the nucleated

cell, or eukaryote—the foundation of multicellular organisms—emerged through a process known as endosymbiosis, where organisms from two distinct domains of life—a bacterium and an archaeon—joined together to form a higher-level unit, the eukaryotic cell, from which all complex life has descended. The original organisms became so interdependent that they could no longer survive independently of each other, and thus became a brand new organism [16]. This event describes what Smith and Szathmáry [17] dubbed a major evolutionary transition (MET). They identify three common features of a MET: "(1) Entities that were capable of independent replication before the transition can only replicate as parts of a larger unit after it… (2) The division of labour: as [Adam] Smith pointed out, increased efficiency can result from task specialization… (3) There have been changes in language, information storage and transmission" (p. 227), examples of which include the genetic code, sexual reproduction, and human language. Szathmáry [18] further characterized METs as events where "independent replicators… form higher-level units… [so that] evolution at the lower-level [becomes] constrained by the higher-level" (p. 10104). In essence, the communion of previously independent units results in the emergence of interdependent and symbiotic feedback loops, which collectively form a larger system that cannot be reduced to its specialized constituent parts. This bidirectional relationship between lower- and higher-level units makes both competition and cooperation relevant to the evolutionary process, creating a tension.

METs are pervasive in evolutionary systems. Many lineages of eukaryotic cells became so interdependent that they could only survive as multicellular organisms, in which increasingly specialized cells die when separated from the body. Many lineages of multicellular animals developed sexual reproduction and could no longer reproduce independently. Some lineages of multicellular organisms, such as humans and social insects, became so interdependent that they could only survive as collective organisms. Most multicellular organisms, including humans, host countless numbers of other species in their guts and elsewhere, known as the microbiome. In many species, neither the microbiome nor the host can survive without each other. In an analogous fashion, archaeans, bacteria, eukaryotes, multicellular, and social life forms collectively generate the ecosystem life support functions required for their mutual survival. This last point explains why humanity must reign in its destructive habits and develop an ecological civilization.

The reality of METs challenges the prevailing view of cooperation as inherently disadvantageous by reversing a key assumption. Specifically, lower-level units are not merely "selfish" replicators exploiting higher-level units for their own preservation and expansion but instead occupy functional roles that support and sustain the higher-level entity upon which their survival depends. In fact, following a MET, the absence of cooperation is a precursor to collapse or death. For example, within multicellular organisms, the breakdown of cooperation among cells disrupts intercellular communication and impairs regulatory mechanisms that prevent unchecked cell division. This breakdown can result in cancer, which ultimately destroys both the 'selfish' cancerous cells and the higher-level organism [19].

At the species level, individual organisms can become so entangled and specialized that they effectively form a single, integrated, cohesive, higher-level superorganism. When this happens, a species is considered "eusocial" [20]. Prominent examples of species that have undergone a MET into eusociality include ants, termites, and bees. In ants, colonies are complex, compartmentalized social structures with highly specialized members that exhibit distinct morphologies (castes). Besides the reproductive queen, worker ants form specialized platoons that carry out divisions of labor. Some platoons function like the immune system, defending the colony and attacking invaders, while others resemble the endocrine and circulatory systems, transporting chemical signals and materials throughout the colony. In this analogy, individual ants correspond to cells, ant platoons to organs, the relationships between platoons to bodily systems, and the colony to a single organism. For example, in some taxa of social insects in which larva play a role in determining their future cast, the "overproduction of reproductive individuals at the expense of workers [can occur], with significant costs to colony fitness" [21] (p. 387).

Eusociality does not render competition moot. Just as a defective cell or gene can flourish by undermining the body, a defective individual—whether an ant or any species that underwent a MET—can succeed by draining the health of the group.

While relatively rare, species that have undergone METs make up a substantial percentage of Earth's total biomass and exert dominion over vast resources [22]. Given humanity's unmatched social nature and ability to cooperate, an important question arises: have humans also undergone a similar MET? Is human society a higher-level organism, akin to ant, termite, and bee colonies? Smith and Szathmary [23] explicitly applied the term they coined to primate and human societies. Wilson [24] similarly states that "it appears likely that human evolution was a full-fledged [MET]", wherein the species' "primate ancestors became the… equivalent of a single organism" (p. 135). In this view, human society is a superorganism bound together by extreme cooperation—not the simple aggregation of competitive individuals. Unlike other species that underwent an MET, the human transition is culturally mediated. Yet, as with other eusocial species, competition remains important. Alongside cooperative evolutionary pressures that have helped align the interests of individuals and groups, competitive pressures have also molded individuals to succeed at the expense of their groups.

2.3. Multilevel Selection: The Rise, Threats, and Maintenance of Human Cooperation

The competitive-cooperative duality inherent to human evolution raises several questions about the processes and mechanisms that could have facilitated and sustained a MET toward eusociality. Competition can pay large dividends to individuals who hoard resources for themselves even when sharing would enhance the group's overall fitness [25]. This misalignment of incentives gives rise to social dilemmas, where individual and group interests are at odds—a challenge faced by all social species. How, then, are these competitive forces balanced with cooperative forces in human societies? When does one take precedence over the other?

Darwin [26] speculated that "When two tribes of primeval [people], living in the same country, [come] into competition... the one tribe [that] include[s]... a greater number of courageous, sympathetic, and faithful members, who [are] always ready to warn each other of danger, to aid and defend each other... would without doubt succeed" (p. 162). This phenomenon exemplifies multilevel selection (MLS), tersely summarized by Wilson and Wilson [27] as a situation where "selfishness beats altruism within groups" and "altruistic groups beat selfish groups" (p. 345).

Within any given population, individuals can be cooperators or defectors. Cooperators sacrifice their wellbeing by paying a cost to provide a benefit that increases the population's average wellbeing. In contrast, undetected defectors reap the benefits generated by these cooperators without paying any short-term cost, thus achieving higher payoffs than their cooperative counterparts. Over time, as the relative advantage of defectors continues to exceed that of cooperators, defection should become the evolutionary stable strategy, leading to the gradual erosion of cooperation. In game theory models, groups containing fitter individuals—those with the highest payoff—will split faster and more frequently. However, if a population is subdivided into enough groups that can either remain intact or split, a higher-level selection process called "group selection" can emerge with sufficient variation. Here, groups with a higher proportion of cooperators can exhibit greater cohesion and longevity, enabling them to compete more effectively against groups dominated by defectors. One form of cooperation, in fact, is to punish non-cooperators, which explains why many players in an ultimatum game will reject offers under 30% of the pie: they altruistically sacrifice their own utility to punish selfishness, which deters selfish behavior by making it less adaptive since selfish players know they will be punished if caught. This dynamic allows cooperative groups to remain evolutionarily viable, thereby preventing their displacement by purely self-interested individuals.

As Wilson [28] observed, these forces of individual and group selection represent two extremes of a continuum across which natural systems operate. Building on this, Traulsen and Nowak's (2006)

mathematical model demonstrated that the right population structure can produce a benefit-to-cost ratio exceeding the critical threshold for cooperation to be selected at the group level, while competition at the individual level is selected against. With that said, even in dictator game scenarios—where individuals face no personal costs and freely decide how to divide and share a resource pool with others without fear of veto or retribution—MLS has been shown capable of supporting the evolution of fairness [29]. This suggests that the conditions favoring cooperation over competition are multifaceted, context-specific, yet both possible and frequent.

The evolutionary backdrop behind the development of anatomically modern humans is defined by robust cooperation—not just individual competition. From the earliest stages, hunter-gatherer societies flourished in settings where routine cooperation among genetically unrelated individuals conferred an advantage on their group over less cooperative groups. For instance, Sober and Wilson [30] argued that the entire hunter-gatherer mode of social organization exemplifies MLS. Hunters shouldered the investment costs of resource acquisition—especially food—for the benefit of others, while other individuals—including gatherers—were required to forgo the potential gains of resource stockpiling and share with the rest of the group. This kind of cooperation facilitated coordinated foraging missions across many societies, enabling groups to exploit their specialized niches for acquiring elusive, nutrient-dense foods essential to the development of the human adaptive complex [31]. Here, cooperation acted as an effective risk-reduction strategy for addressing the stochastic nature of food availability and reproductive success. Although the payoff of self-aggrandizement, scrounging, and hoarding is tempting for individuals, it was easily detected and punished in small scale hunter-gatherer societies where everyone knew each other. Punishments included ostracization from the community, which usually meant death since humans cannot survive apart from their group. This reinforced the spread of prosocial behaviors—such as humility and sharing—along with practices like equitably pooling and redistributing resources, helping to mitigate the uncertainty of capturing prey and obtaining high-calorie foods. It is worth noting that both sharing and punishment of hoarding are both forms of reciprocity, a point to which we will return later.

Since the time of early hunter-gatherer societies, however, the human enterprise has grown exponentially, with both population and economic output reaching ecologically unprecedented levels. Simultaneously, the size of many human groups has expanded to unparalleled scales. Today, state societies are a dominant mode of social organization, encompassing populations that range from a few hundred thousand to nearly 1.4 billion people. This growth has allowed increasing specialization and elevated the scale of human cooperation to record levels. What role, if any, has MLS played in driving this phase of the human MET? How has cooperation persisted, and how have groups avoided complete breakdown as the scope and complexity of human society have entered uncharted territory?

While genetic evolution undoubtedly sculpted human beings with the biological architecture that enables cooperation, it is unlikely that large-scale human cooperation evolved through selection on genes. The genetic composition of the human species is fairly uniform [32]. Genetic mechanisms are inadequate to explain the diversity of social structures and why cooperation among unrelated individuals has persisted and grown to the heights observed in modern societies, because there isn't sufficient variation. However, MLS may sustain high levels of cooperation by exerting a strong influence through cultural rather than biological pathways—shaping social outcomes such as coordination, stability, and institutional resilience rather than genes [33]. In other words, culture is a key ingredient to the human evolutionary recipe, whereby cooperation can emerge as an advantageous strategy by promoting the adaptiveness and resilience of groups.

There are three necessary and sufficient conditions required for natural selection to be activated: (1) variation; (2) differential survival; and (3) an inheritance mechanism. Culture fulfills all three of these conditions. For the purposes of this article, we define culture as collective and cumulative norms, identities, values, institutions, technologies, and knowledge—more than can ever be developed by a single generation or acquired by a single individual over the course of a lifetime. Had he dedicated his lifetime to the

challenge, Einstein could not have mastered all the knowledge required to produce the pencils he used when writing down his theories.

In terms of variation, human groups exhibit significant cultural diversity, which surpasses genetic diversity. Because most non-Africans descended from small populations that migrated out of Africa 50,000–70,000 years ago, the genetic variation among non-Africans is dwarfed by genetic variation within Africa [34]. Yet, through cultural evolution, this genetically homogenous group has culturally diversified and adapted to almost every habitat on Earth. Furthermore, variation between cultures—for example, between Inuit elders and Wall Street executives—can exceed variations between individuals within a culture.

Second, in terms of differential advantage, the benefits conferred by specific cultural traits directly affect the success and persistence of the groups that adopt them. Certain cultural structures prove more adaptive in specific social, economic, and ecological contexts than others [35,36]. For instance, knowledge of securities laws and the ability to exploit the carried interest loophole give hedge fund managers a distinct selective advantage on Wall Street, while Inuit elders possess a clear selective advantage in understanding whale migration patterns and combining ice and caribou skin to build insulated igloos in the Arctic. Throughout human history, societies with cultural structures that most effectively forged and enforced cooperation often outperformed societies whose cultural structures did not. For example, Turchin [37] argues that the fate of many agriculturalist and pastoralist societies during times of warfare often hinged on their ability to foster cooperation more effectively than their rivals. Similarly, Wilson [38] observes that many popular religions function as group-level adaptations, promoting cooperation and reducing free-riding, particularly during intergroup conflict.

Finally, two inheritance mechanisms are profoundly important to the transmission of culture: behavioral and symbolic [39–41]. Behaviors are passed down through social learning in many species. For example, Sulfur Crested Cockatoos have recently learned from each other how to open garbage bins in Australia [42]. Symbolic learning, based on language and the communication of abstract ideas, is the most important. It is poorly documented outside of humanity, though recent studies suggest that the vocalizations of Sperm Whales—another highly social mammal—have many attributes of language [43]. These mechanisms allow for the construction and enforcement of social norms, the cultivation of shared identities, and the establishment of collective decision-making forums, all of which serve to instill ethical values that sustain prosocial behavior [44]. As societies expanded in size and density, institutions evolved to coordinate activity between geographically disconnected individuals [45], including religions and national identities that increased trust among anonymous individuals. The emergence of money helped coordinate economic activity with anonymous individuals regardless of trust [46]. These mechanisms can serve either to tame competition and promote cooperation or, conversely, to amplify competition and allow cooperation to erode.

Taken together, it is possible that cooperation has flourished at increasingly larger scales due to MLS pressures, with group selection emerging from cultural phenotypic variation and effectively counteracting individual selective advantages that favor competition. As a result, humanity is now organized into a socio-ecological hierarchy (SEH)—a nested series of interconnected groups that collectively form a complex structure with multiple levels of organization. This SEH spans from individuals to firms, communities, states, and the international community. The various subsistence practices, trading partnerships, financial flows, and exchange relationships within the SEH constitute the global economy, in which numerous institutions at each level mediate interactions among agents. These agents strive to extract resources, transform them into economically useful products, and allocate them toward alternative and desirable ends. Just as MLS pressures balance cooperation and competition, could these same forces be influencing the organization of the global economy—shaping behavioral incentives, how economic institutions function, the flow of resources, and the long-term success or failure of agents?

3. The Global Economy as a Multilevel Selection Process

Because of MLS, self-interest and competition may yield the highest economic payoff at lower-levels of the SEH, while cooperation becomes more profitable at higher-levels. The interaction between these pressures organizes economic activity by selecting some agents over others. In this section, we illustrate these MLS dynamics with some examples of the tensions and complementarities that arise between agents at different scales across the SEH.

3.1. Individuals

As previously stated, human knowledge is collective and cumulative. The knowledge required to survive even the most hospitable climate in the world is more than any individual human can master. Even highly trained individuals with access to artifacts produced by thousands of people using knowledge created by millions of people over millennia—such as clothing, a knife, a bow and arrow, a rope—cannot survive for long on their own. As Henrich [47] has chronicled, even the technologies of small hunter-gatherer bands were distributed across many individuals, and the loss of just a few of them could mean the loss of the technology and the band's ability to provision its basic needs. Individual humans, separate from their cultures, can survive no better than a human cell apart from the body. In a small enough community with just enough individuals to contain and sustain the knowledge required for their survival, failure of any single individual to cooperate in provisioning basic needs doomed the group. The payoff matrix for this social dilemma is one in which every quadrant except mutual cooperation is death.

Things become more complicated in larger groups, in which it becomes possible for some individuals to benefit from the cooperation of others while keeping all they produce to themselves (defection). Our next two sections explore two types of larger groups, communities and firms, which are two distinct approaches to provisioning, through the lens of MLS.

3.2. Communities

Within communities, the most self-interested individuals tend to outcompete their other-regarding counterparts, often to the detriment of the communities they belong to. However, between communities, those that are most cooperative—focused on the welfare of the collective—outcompete those that are more fragmented by within-group selfishness.

For most of human history, selfish behavior meant failure to share one's food [30]. Most early humans lived in small communities defined by Dunbar's number, which is the number of individuals a primate can meaningfully get to know well enough to identify as cooperators or defectors. Dunbar's number scales with brain size and is about 150 for humans. The need to detect cooperators and defectors likely contributed to the evolution of human intelligence and of gossip [48]. Abundant anthropological evidence indicates that most small bands punished those who failed to share food, with ostracization—often equivalent to death—frequently the fate of repeat offenders [30].

While the payoff for non-cooperation is extremely negative in small bands, the cost of cooperation is often low and the payoff extremely high. For many types of hunting and gathering, rewards come in large units. A hunter kills an elk, or a gather finds a fruit tree with far too much ripe fruit for one person to eat. If food is costly to preserve, the marginal benefit of food to someone with a surplus is very low, while the marginal benefit to someone with a deficit is very high. Collective utility is clearly maximized when food is equitably shared. Reciprocity is so strong in human cultures that for most people it is an automatic response [49]. Thus, the hungry recipient of a gift of surplus food feels an obligation to reciprocate in the future for an invaluable gift, while the cost to the giver is negligible. Each economic exchange not only maximizes utility but also strengthens social bonds [50,51].

Prior to the emergence of money, most economies were deeply embedded within social structures built on gifting and reciprocity. Though these economies exhibited considerable diversity, one common aspect is non-synchronous, qualitative exchange, in which the recipient of a gift reciprocates at an unspecified later date with a different item of similar value to the one originally received. Reciprocity can also be indirect, extended to others in the community rather than the original gifter. Gift economies prioritize fairness over time [50–52].

Cooperation at larger scales than Dunbar's number offers significant social advantages despite individual costs. Self-defense is perhaps the most obvious example. Larger groups are less likely to be attacked than smaller groups and more likely to win if attacked, but individual defenders risk death. Numerous technologies also require larger, more specialized populations to conceive of, build, deploy, and maintain. Irrigation, large-scale agriculture, and the construction of large buildings are clear examples. To achieve cooperation at the necessary scale, cultures had to evolve institutions that enhanced trust and punished selfish behavior across individuals who might not know each other personally.

Ostrom [53,54] identified eight core principles for managing common pool resources, a classic example of a social dilemma. Wilson, Ostrom, and Cox [55] generalized these into eight core principles for successful cooperation in groups, including groups of groups, explicitly linked to MLS:

1. Clear group identity and shared sense of purpose
2. Equitable distribution of benefits and resources
3. Inclusive decision making
4. Transparency of behavior
5. Graduated responding to helpful and unhelpful behavior
6. Fast and fair conflict resolution
7. Autonomy and authority to implement CDP1-CDP6
8. Appropriate relations with other groups (consistent with CDP1-CDP7) [41]

Close identification with a shared religion or with shared culture specific phenotypes such as language, dress, adornment, and shared stories enhances group identity, facilitating cooperation with individuals one does not know personally. Graduated responding to helpful and unhelpful behavior includes social sanctions against defectors and rewards to cooperators, including greater attractiveness to mates. Monotheistic religions, which arose in the Middle East together with urbanization, are characterized by belief in an omnipotent, all-seeing god that will know if individuals disobey 'the golden rule' and can punish defectors in the afterlife, further encouraging cooperation [38].

Even in modern times, our economic relations with our families, friends, neighbors, and broader community are often built on gifting and reciprocity. Parents rarely charge their children room and board. No one would consider inviting friends over for dinner and then charging them. Neighbors do favors for each other. Civic virtue means putting the needs of the group ahead of the individual. Civic duties are the obligations we have to each other to ensure the well-being of our communities. In such exchanges, we often feel bad if we receive more than we gave. We seek fairness rather than advantage.

3.3. Firms and Corporations

Shared identities and purpose, ethical obligations, and a sense of fairness bind communities together. This limits the size of the cooperative group and hence the degree of specialization possible, which in turn limits economic possibilities. Without social ties and trust, an economy built on asynchronous, qualitative reciprocity is not possible. Money, however, allows for synchronous, quantitative reciprocity with no need for trust in anything but the money itself, and can coordinate economic activity across vast numbers. This allows for much greater specialization and the production of far more technologically advanced commodities, such as cars, sophisticated electronics, and jet airliners. Economic exchange takes the form

of a good or service sold for money. Exchange does not create meaningful social ties. We do not write thank you notes to supermarkets.

While market exchange is voluntary and in that sense fair, actors in a market economy typically strive to get the best deal possible, rather than the fairest. Each side in a transaction seeks to profit at the expense of the other [51]. Most people are delighted to buy something for 80% off, even if we know the price we pay means that both labor and nature were exploited.

Firms and corporations are production units primarily focused on maximizing profits or increasing market power. Milton Friedman famously argued that social responsibility for firms is a "fundamentally subversive doctrine" and "there is one and only one social responsibility of business—to use its resources and engage in activities designed to increase its profits so long as it stays within the rules of the game" [56]. However, economically powerful firms regularly lobby politicians to change the rules of the game with great success [57,58]. While Friedman's doctrine is losing support, it remains a fairly accurate description of most businesses [59]. They purchase inputs and labor from other firms at the lowest prices they can pay and lay off employees if doing so increases their profits. They sell their products at the highest price they can charge, while consumers seek the lowest price they can pay. Most firm employees seek the highest wage they can possibly get.

Mainstream economics textbooks claim that everyone acting in their own self-interest leads to the greatest good for all, at least in the absence of social costs not paid by firms. However, such social costs are ubiquitous and include environmental harms; illness, accidents, and death from poor working conditions; social disruptions from unemployment and growing inequality; and so on. Self-interested firms routinely shift these costs onto society for their own benefit [60–62].

Mainstream textbooks also claim that in a market economy, competition between firms will drive economic profits to zero. If true, this would clearly not be in the best interest of the individual firm. There is, therefore, a strong incentive for firms to seek monopoly power or collude with others to set prices.

Ironically, mainstream economics downplays the importance of monopoly power, which is rarely mentioned before chapters 9 or 10 in most mainstream economic textbooks. The theory of market competition assumes rising marginal costs for firms, in which case smaller firms would have lower production costs than larger firms, thus favoring market competition. Overwhelming empirical evidence convincingly shows the opposite. The modern economy is dominated by a handful of extremely large firms, and smaller firms must grow or die. The reason for this is that most firms exhibit increasing returns to scale [63–68]. As industrialist Andrew Carnegie observed, "cheapness is in proportion to the scale of production" (quoted in [69]).

The rewards of cooperation between firms to maintain profits, or of selfish firms to acquire monopoly power are so high, along with the negative impacts on the rest of society, that most countries have anti-trust laws to prevent both. Unfortunately, in the United States (U.S.) and many other places, these laws have been poorly enforced since the 1980s, and we have witnessed a corresponding increase in both market power and economic inequality [69].

Market economies and microeconomic theory are both focused on the self-interested individual or firm. However, the importance of social dilemmas in economic activity, such as climate change, most other forms of pollution, biodiversity loss, soil loss, ocean acidification, the paradox of thrift, inflation, and more, have skyrocketed since the core principles of microeconomic theory were first developed in the 1870s, revealing the high social costs of selfish behavior and the need for states to represent the collective interest.

3.4. States

Firms and corporations cannot exist without a state to enforce private property rights and other legal contracts. States also make critical investments in basic research and other forms of R&D that have proven critical to the development of advanced technologies such as nuclear power, the Internet, and many of the

marvels of modern electronics [70]. These goods and services may have been made more ergonomic because of firms and corporations, but they only exist in the first place because of state activity. Imagine what the modern capitalist economy would look like if states hadn't spent decades developing the internet—the cornerstone of almost all industries and activities? States construct and maintain the legal, physical, and epistemic infrastructure without which modern private-sector activity could not function. States also manage national defense, environmental protection, and public infrastructure—all of which are essential to both businesses and citizens—and address major economic problems such as inflation and unemployment. States also compete with other states for access to territory, resources, and markets. MLS theory sheds considerable light on the numerous social dilemmas inherent to these activities. The basic arguments remain the same: self-serving individuals and firms may outcompete their more benevolent counterparts within states, but the states with more cooperative members outcompete states with fewer.

For example, taxes are critical to modern state societies to bureaucratically function, provide essential social services and other public goods, protect the environment, and foster healthier citizen-state relations. However, tax cheats may do better personally than taxpayers. This creates a classic social dilemma: agents bear a cost to benefit others, but failure to pay taxes results in states losing its capacity to govern, thereby reducing its ability to achieve social goals and deliver the public goods necessary for citizens and firms to function.

Because levels of tax compliance and enforcement vary across states, cross-country differences in cooperation between individuals and the state are heavily shaped by tax attitudes—attitudes that are, in turn, influenced by a society's social norms [71]. While institutional design—such as specific tax laws, rates, and penalties—does impact levels of compliance, social norms serve as mediating variables that can either amplify or suppress tax evasion. For example, Górecki and Letki [72] found that "increasing [the] tax rate lowers the probability of evasion as long as one views "most others" as honest taxpayers, which highlights the importance of equitability (fairness) concerns for tax compliance decisions" (p. 727). That is, individuals who perceive others as following tax laws are more likely to internalize that behavior as a social norm and, consequently, are more inclined to comply themselves [73]. In contrast, individuals who are under the impression that their fellow citizens do not respect the tax code increase incidents of free riding. Revealing how group selection operates on cultural variation, Wenzel [74] shows that the effect of social norms on tax compliance strengthens as individuals' identification with a reference group increases.

The issue of tax compliance reveals a key MLS dynamic: while an agent who avoids paying taxes may be materially better off than a cooperative citizen, states with more cooperative citizens and higher tax compliance rates tend to function more effectively than those with lower rates. In these more cooperative states, stronger social norms and a shared sense of national identity often frame taxpaying as both common and important, thereby strengthening governance by increasing citizen trust, tax compliance, revenue, and institutional capacity. This allows states with more cooperative citizens to outcompete states with more selfish citizens. Moreover, states that more effectively deter tax avoidance and evasion typically have robust agencies—which are group-level adaptations—capable of monitoring tax behavior, penalizing free riders, and setting tax rates that are perceived as fair and enforceable.

In summary, the state is the domain of macro-economics, intended to serve the collective needs of its citizens. Sadly, this outcome often suffers in states where firms and individuals can freely donate to politicians' election funds, leading states to favor the interests of the wealthy over the rest [58].

3.5. The International Community: Humanity

As we move from states to the international community, we leave the domain of natural selection. There is only one international community. However, humans are capable of intentional cultural evolution. More than any other species, humans have the capacity to imagine different futures and move towards those perceived as the most desirable [75]. MLS still has much to teach us.

We begin by stressing the growing interdependence between states, facilitated by money, which is rapidly becoming so widespread that humanity may be undergoing another MET into a global superorganism [76]. The dramatic weakening of international supply chains during COVID-19 helps illustrate how interdependent humans have become [77]. Astonishingly few goods are produced entirely within a single nation's boundaries. International interdependence has never been so high.

Despite this interdependence, many states prioritize their own welfare over that of humanity. Among the most extreme forms of this are imperialism and colonialism, in which powerful states seize the territory and resources of less powerful states, typically with dire consequences not only for the imperialized and colonized states but also for humanity. One study estimates that in the period from 1990–2015, the net appropriation of resources by the Global North from the Global South—a transfer of resources from the poor to the rich—was $242 trillion (2010 constant dollars) [78]. It long seemed that economic imperialism had displaced imperialism and traditional colonialism, but Putin's invasion of Ukraine and Trump's attempted seizure of Venezuela's oil and threats against Greenland, Mexico, Colombia, and other countries may be initiating a return to 19th-century international politics, which threatens to destabilize the global system.

Climate change may nonetheless present the ultimate global social dilemma. Confronting climate change requires a systemic transformation—a titanic shift in social organization—sufficient to ensure that total (absolute) greenhouse gas (GHG) emissions decline, not merely emissions per unit of GDP (relative). This transformation must also occur within a narrow time frame to avoid crossing the critical tipping points of 1.5 and 2 degrees Celsius. Moreover, a few powerful states are responsible for the majority of cumulative GHG concentrations. Among the states that are beginning to emit more, their per-capita emissions are generally low, or their emissions are primarily driven by survival needs rather than luxury.

Individual states face a choice: they can either cooperate by reducing their domestic GHG emissions or defect by refusing to do so. States that reduce emissions are likely to undergo slower economic growth or even experience degrowth, which can increase their vulnerability to the imperialism of the strongest nations. This presents a classic social dilemma: states must choose whether to forgo potential economic and national security gains from fossil fuel investments for the benefit of the international community or to defect in pursuit of self-interest—an approach that entails disregarding the unevenly distributed and intergenerational consequences of GHG emissions.

In 2009, this collective action problem led the U.S. Congress to reject the "American Clean Energy and Security Act" (the Waxman-Markey Bill), a cap-and-trade proposal by Representatives Henry Waxman and Edward Markey. After being momentously passed by the House of Representatives, the bill never even made it to the floor of the Senate because policymakers perceived a tradeoff between the U.S.'s short-term economic interests and long-term climate stabilization, which aligns with the international community's long-term interests [79]. Many senators argued that foreign leaders and industries would exploit the United States' carbon price by increasing their production of carbon-intensive, lower-cost goods, thus putting the U.S. at a competitive disadvantage. Others spoke of U.S. energy dominance and national security as reasons for rejecting the bill. Years later, under the Trump administration and its "America First" platform, this attitude has become even more pronounced and morphed into a form of nationalism that not only shows contempt for climate change action and any attempt to regulate fossil fuel production [80] but also a willingness to seize control of other countries' oil.

Thus, in line with MLS, self-serving states that prioritize their own interests outcompete more cooperative states that are willing to take robust climate action or respect the territorial sovereignty of other states. In the long run, however, these non-cooperative states threaten runaway climate change with dire consequences for all—including themselves—and a return to the barbarities of colonialism, which creates socially costly, dire political and economic turmoil. International efforts to reduce climate change, such as the Intergovernmental Panel on Climate Change (IPCC), lack sufficient enforcement mechanisms to penalize free riders. Perhaps cooperative states that provide mutual aid and other forms of assistance will

be better equipped to adapt than self-serving states. However, the greater the proportion of free-riding states relative to cooperating ones, the less emissions are reduced, and the more severe climate change becomes, thereby further weakening the international community. This is why culturally evolved group-level adaptations—such as norms that name, shame, and embarrass states that renege, institutions that create space for negotiation and establish rules of conduct, and legal instruments that compel compliance and sanction violators—are essential for shifting the benefit-cost ratio in favor of cooperation over competition.

3.6. The Global Ecosystem

The global ecosystem can be conceived as the group of all species on the planet, which collectively generate the life support functions essential for all species. Cooperation between states can help humanity flourish in the short run, but if this flourishing leads to larger and larger human populations, greater consumption per capita, and a greater capture of the planet's net primary productivity, it will threaten the vital ecosystem services upon which all life depends. Humans and their livestock already account for 96% of terrestrial vertebrate biomass [81]. Humans have achieved this by drawing down planetary stocks of plants, animals, minerals, and fossil fuels much faster than they regenerate, and spewing waste faster than it can be absorbed [82–84]. Even current levels of economic activity cannot be sustained. This represents the greatest social dilemma possible, though in this case, it appears that, unlike humans, most other species are already cooperating, in that they are not exceeding their carrying capacity and drawing down the accumulated resource stocks that sustain them.

Though humans may currently be the lone defectors, humans are not the first species (or group of species) to exceed the Earth's carrying capacity. Early in the evolution of life on Earth, cyanobacteria evolved when the Earth's oceans and atmosphere were largely anaerobic. Cyanobacteria use solar energy to transform water and carbon dioxide into carbohydrates, with oxygen as a waste product. Oxygen is toxic to cyanobacteria and most other species alive at that time. The oceans of the time were rich in unoxidized iron, which quickly captured the free oxygen. However, as soon as the rate of oxygen emissions exceeded rate at which new unoxidized iron entered the system, it was inevitable that the iron would be depleted, allowing the oxygen to accumulate until it killed off the cyanobacteria and other oxygen sensitive species. Between roughly 2.5 and 2 billion years ago, this happened repeatedly, culminating in the permanently oxygenated atmosphere, which allowed for the evolution of aerobic organisms [85]. Similarly, forests evolved during the Devonian period, before the evolution of fungi capable of breaking down lignin. The forests rapidly sequestered carbon dioxide from the atmosphere, possibly driving the subsequent global cooling and mass extinction [86].

A logical conjecture is that species that grow explosively at the expense of the ecosystems into which they evolved soon drive their own extinction. This explains why most species 'cooperate' to sustain the global ecosphere. Humans, a still young species, may be an outlier doomed to early extinction if changes are not made.

What can be done about this? As is the case with global climate change, humans must change their relationship to the global ecosystem. The proper relationship is one of gifting and reciprocity, as has been practiced by many cultures throughout human history [87–89]. Ecosystems bestow gifts of infinite value upon humanity, and humanity must reciprocate by taking only what is needed for our secure sufficiency and working to restore the harm already inflicted on these systems. The relationship between humans and the rest of nature should be the same as that between a human cell and the human body [90].

The right relationship between humans and the rest of nature is the domain of ecological economics and an essential element of an ecological civilization.

4. Discussion

For most of human history, people lived in small bands of hunter-gatherers, where cooperation was essential to the species' success and its ability to inhabit diverse, rapidly changing terrestrial biomes. Today, with a global population of 8 billion, humans exist in an interconnected, hierarchically structured global economy. Dubbed the SEH, this system comprises individuals, communities, firms, states, the international community, and global ecosystems at the top. No agent can function independently of the higher-level groups in which they are embedded.

A consequence of this new organizational arrangement is that social dilemmas pose systemic risks that could collapse the entire system. When a lower-level agent prioritizes their own interests at the expense of higher-level ones, crises can emerge. In other words, while selfishness is often profitable in the short-term for the defecting agent, excessive selfishness at lower-scales is ultimately self-defeating because it undermines the welfare of groups at higher-scales upon which those agents depend. MLS suggests that the only prophylactic against such dilemmas is cooperation at the appropriate scale. The scalar dimension that MLS introduces to the evolutionary process gives scope to the relative advantages and disadvantages that competition and cooperation offer within the structure of the SEH. The dual selection pressures of competition and cooperation create distinct benefit-to-cost ratios with far-reaching implications. Due to the inherent tension between the fitness of lower- and higher-level agents, the prevailing selective force depends on the situational context and the scale being considered. At certain levels of the SEH, competition may confer advantages while cooperation incurs disadvantages. Conversely, at other levels, cooperation may prove more advantageous, with competition being less beneficial—or even catastrophic.

The fact that MLS serves as an organizing force behind the global ecological economy carries two major implications. First, in such an interconnected and highly sensitive system, cooperation is needed at increasingly higher-scales to preserve the integrity of the global economic system—thereby increasing its overall fitness. Second, the scale of a problem should guide policy design. The level of the SEH predominantly impacted by a social dilemma, along with the ripple effects of policy responses across levels, should determine which behaviors are rewarded and which are punished. When competition at lower-levels threatens to reverberate across the SEH and negatively impact higher-levels, selection pressures should be aimed toward subordinating the short-term interests of lower-level agents in favor of the long-term interests of higher-level agents.

The most important level of socio-ecological organization that has been neglected—and now requires urgent attention—is the global ecosystem. The entire SEH exists within the global ecosystem, whose life-support systems and services sustain humans and all other species. Until now, humanity has committed itself to perpetual economic growth, endlessly extracting finite resources and profligately consuming goods and services. International institutions such as the World Bank, International Monetary Fund (IMF), and even the United Nations (UN) have largely endorsed this trajectory. However, in line with MLS, this self-interested behavior at the scale of the human species continues to inflict profound harm on the global ecosystem, and all it reproduces—including humanity itself.

This raises a practical and consequential question: do existing social and economic structures actually enable humanity to cooperate with itself—and with other species—to rehabilitate the global ecosystem, understood as 'the group of all groups'? Much of today's ecological crisis can be traced to a small number of imperial and colonial metropoles that continue to monopolize a disproportionate share of planetary wealth, particularly the material and energy stocks that sustain modern societies. This concentration of power has produced an ecologically unequal exchange between less economically and militarily powerful states and the metropoles that have systematically dispossessed them. Moreover, modern states themselves have increasingly been co-opted by financial actors and corporations, which leverage their investments and

resources to pressure state authorities to forgo ecological repair and instead deploy public power in the service of continued capital accumulation.

Taken together, these dynamics generate a multi-layered social dilemma. MLS provides both an explanatory framework for understanding it and a prescriptive guide for addressing it. Financial actors and corporations that induce states to prioritize capital accumulation over institutional capacity, public welfare, and ecological repair may gain a competitive advantage over more altruistic and environmentally oriented actors. Similarly, states—the social unit operating above corporations and financial actors—that pursue narrow self-interest at the expense of the all-encompassing global ecosystem can outcompete weaker or more cooperative states. Yet MLS also implies a countervailing dynamic: groups of altruistic citizens, organizations, and states can outperform groups of self-serving financial actors, corporations, and states. This is because selfish behaviors in a hierarchically nested system like the SEH are self-defeating in the long-run. Weak state institutions foster political instability, degraded infrastructure, and inadequate legal protections, producing a fragile operating environment even for corporate and financial actors. At the same time, ecological overshoot and declining ecosystem services erode the life-support functions and deplete the very resources upon which all humans—including the financial actors, corporations, and the most powerful states—ultimately depend.

Of course, so long as the balance between competition and cooperation remains skewed toward competition, the cooperative efforts of altruistic actors are unlikely to be sufficient to avert global ecological crises, even if such actors may prove more resilient by providing mutual aid to one another. Overcoming this structural barrier requires, as MLS theory suggests, an overhaul and evolution of the global economic system toward more robust forms of group-beneficial cooperation. While such a transformation is undoubtedly daunting, human history is neither linear nor deterministic; a wide range of social organizations have existed in the past and continue to exist today [91]. This social and historical variability indicates that the reorganization we propose is feasible. Achieving such a transition, however, necessarily entails several interrelated steps.

First, economically and militarily weaker states—particularly those in the Global South—must cooperate by forming new coalitions that reduce their structural dependence on, and thus the leverage of, powerful self-serving actors that exercise disproportionate control over global resource flows [92]. Second, new moral and ethical values must be cultivated—ones that place the interests of the biotic community, of which humans are just one member species, above those of the international community and all other lower-level groups along the SEH. As we previously emphasized, this new relationship between humans and the rest of nature should be akin to the relationship between a human cell and the human body. Lessons can be humbly learned from many Indigenous societies, such as the Haudenosaunee, who have adopted this ontology with great success for thousands of years [93]. Third, new social and economic institutions must be culturally constructed at the scale of the global ecosystem to prioritize the health and integrity of functioning ecological processes [90]. For example, a global commons regime that treats ecosystem services and their underlying biophysical structures as common property of present and future generations of humans and other species could be established. This commons regime could establish an ecological container around the global economy to shrink economic throughput and waste to levels commensurate with ecosystem needs, all while ensuring a more just distribution of resources both between and within levels of the SEH [94–96]. Fourth, the relative benefits of cooperation must be increased, and the costs of competition and free-riding raised, through the development of instruments that more effectively monitor, detect, and punish selfish behavior. For instance, while many states currently submit greenhouse gas inventories to the United Nations Framework Convention on Climate Change (UNFCCC) on a voluntary basis, such reporting could be made compulsory, with states that fail to meet ecologically informed but socially negotiated emissions targets subject to enforceable sanctions. Under such a regime, not only would defectors be penalized, but states that fail to participate in enforcing sanctions would also face penalties,

thereby reinforcing cooperation across multiple levels [97,98]. In MLS terms, these norms and institutions would strengthen higher-level selection pressures enough to override lower-level selection pressures.

While forging such an ecological civilization is undoubtedly a herculean task, the alternative is the widespread collapse of ecosystems and profound devastation for humans and millions of other species. As Farley and Kish [99] have argued, in an era of "unknown unknowns", where human activity is driving changes in the global ecosystem faster than both their future states and probabilities can be modeled, it is crucial for ecological limits and thresholds to begin defining the boundaries of economic activity—just as Herman Daly [100,101] has long advocated. Without such constraints, irreversible tipping points will be crossed, triggering feedback that loops propel humanity into a downward social and ecological spiral.

In light of these stakes, future research should prioritize identifying and analyzing historical and contemporary cases in which societies have successfully managed large-scale social dilemmas, and then rigorously assess the extent to which these strategies can be adapted, modeled, and tested in modern, complex systems. Moreover, given the immediacy of ecological breakdown, greater attention must be paid to the temporal dynamics of MLS, particularly to how the costs and benefits of cooperation are distributed across time, to design institutions capable of balancing short-term individual costs with long-term group benefits.

5. Conclusions

Competition undoubtedly plays an important role in the global ecological economy at every level of the SEH. At the lowest-levels, humans have undergone a major evolutionary transition and must cooperate to survive. Humans have evolved numerous cultural traits that encourage cooperation and punish selfishness at the community level, many of which were based on reciprocity. The emergence of money helped coordinate activity among self-interested firms and corporations, leading to a market economy, the domain of microeconomics, intended to serve self-interested individuals. At the next level, states compete for access to and control over global resource flows, often by claiming sovereign spaces rich in energy reserves and critical mineral deposits as their territory. These same states also try to leverage their material base to attract the most private-sector investment and become regional hegemonies. At an even higher-level, the international community competitively displaces other species in search of new habitat space and low-entropy matter and energy.

In addition to competition, however, cooperation is also possible at every level. The history of humanity is one of cooperation at ever greater scales. States bond people together through cultural signifiers such as language, dress, and adornment, as well as shared stories. They broker legally binding agreements to efficiently manage public services, such as waste treatment and transportation infrastructure. States can address common resource challenges, such as water scarcity and regional air pollution. States ratify trade agreements to protect each other's property rights and ensure mutual access to important goods and services. States also form security alliances that respect each other's sovereign territory, in which member states defend one another's domestic resources against mutual adversaries and establish prices for key commodities, such as oil. And the international community coalesces to enforce treaties that regulate labor and commodity standards, including restrictions on the production and sale of certain materials with global environmental consequences, like chlorofluorohydrocarbons and other refrigerants. This is the domain of macroeconomics.

Building on Dobzhansky's [102] comments that "nothing in biology makes sense except in the light of evolution", we view the global economy as a continually evolving complex adaptive system. Being a hierarchically nested system of agents, we view the global economy as a major evolutionary transition (MET)—a watershed moment in which previously independent entities came together to form a higher-level organism that exists and replicates as a unified whole. Traulsen and Nowak [3] were correct to speculate that multilevel selection (MLS)—a process wherein competitive individuals outcompete cooperative individuals within groups, while cooperative groups outperform competitive groups—is an

"important organizing principle" for structuring "the economics of nations". We argue that culture is the mechanism and source by which humans and the global economy evolve.

In contrast to neoliberal economic theory, which posits that competition between individuals is the primary organizing force of the global economy, MLS gives scope to both competition and cooperation, a widespread human behavior. Whether cooperative or competitive strategies ultimately prevail depends on situational factors and the relative benefit-to-cost ratios. However, we argue that cooperation becomes the most adaptive social behavior at progressively higher-levels of organization, as it effectively resolves social dilemmas—situations in which individual and group interests are in tension.

In an era marked by extreme interconnectedness, interdependence, and ongoing ecological breakdown, a new level of cooperation is urgently needed if we are to achieve an ecological civilization. Cooperative behavior can no longer be limited to enhancing human welfare alone—it must extend to include other species and the ecological processes that constitute the global ecosystem. While the global economy currently operates through cultural structures that serve the interests of individuals, firms, communities, states, and the international community—a model of organization this paper refers to as the socio-ecological hierarchy (SEH)—we call for the all-encompassing and life-sustaining biotic community, which economic activity is embedded within, to now be placed at the top of that hierarchy. This requires humanity to culturally evolve a new series of social norms, identities, rituals, and institutions that favors—indeed, select for—the biotic community and suppresses destructive competition at lower-levels. This is a prerequisite for an ecological civilization.

Statement of the Use of Generative AI and AI-Assisted Technologies in the Writing Process

During the preparation of this manuscript, the authors used ChatGPT in assist in identifying and correcting grammatical errors. All content modified with this assistance was subsequently reviewed and, if necessary, edited by the authors, who assume full responsibility for the full content of the published article.

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Author Contributions

L.G.: Conceptualization; Formal Analysis; Investigation; Project Administration; Resources; Writing—Original Draft Preperation; Writing—Review and Editing. J.F.: Conceptualization; Funding Acquisition; Investigation; Resources; Supervision; Writing—Review and Editing.

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The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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