esa ECOSPHERE

Natural and human economies compared

Geerat J. Vermeij[1,†] and Egbert G. Leigh, Jr.[2]

[1]Department of Geology, University of California at Davis, One Shields Avenue, Davis, California 95616 USA
[2]Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Balboa Ancón, Republic of Panama

Abstract. Human economies and natural ecosystems (natural economies) share fundamental properties. Both are adaptive, cooperative systems where agents—individuals and groups—compete for locally limiting resources needed to live and reproduce. Successful competitors differentially propagate better knowledge and technology for making a living. Competition has favored innovations, diversification (of species or human occupations), higher productivity, greater interdependence among economic agents, and the emergence of more powerful, interactive individuals and groups, so productivity, diversity, and scales of activity have tended to increase over time. Because economic innovations accumulate, these trends have accelerated over time in both natural and human economies.

The shift from mainly genetic origin and transmission of adaptation in natural economies to mainly cultural adaptation among human beings has accelerated these trends dramatically, and made the modern human economy extraordinarily dependent on nonrenewable resources and much more vulnerable to monopolies and tragedies of the commons, internally generated threats less common or less destructive in natural economies. In nature, these internal disruptions are overcome by the advent of new agents, often not involved in causing these disruptions, that compete in new ways. We argue that a comparable shift in societal norms, which govern individual and group status in human society, is needed to keep monopolies and tragedies of the commons from harming both the human economy and the ecosystems on which we depend.

Key words: economy; ecosystems; monopoly; tragedy of the commons; trends.

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† **E-mail:** gjvermeij@ucdavis.edu

Introduction

Most economists have no idea that human economies share essential features with natural ecosystems, and most social scientists resist comparisons between human affairs and the workings of nature because they reject anything smacking of "biological determinism." Nevertheless, ecosystems and the human economy are similar because they are both adaptive systems in which cooperation and competition among individuals for locally limiting resources affect the fates of individuals and groups. Although this similarity has become less obvious as technology and the use of symbols have increasingly enabled humans to cooperate and compete ever more precisely on ever wider scales through intelligence and foresight, close parallels remain in how human and natural economies develop and work. These economic systems all represent variations on a common theme: a network of life-forms that interact with one another by performing different, often complementary functions. Neither individuals within economies nor different economies within the biosphere as a whole are independent; they are linked through intricate interdependencies that are shaped by competitive and cooperative relationships.

Based on Adam Smith's (1776) economic insights and our own previous work (Vermeij 1999, 2004*a*, 2009*a*, Leigh and Vermeij 2002, Leigh 2008, 2010*a*, 2010*b*, Leigh et al. 2009), we compare human economies with ecosystems (natural economies) in order to understand the peculiarities and vulnerabilities of the modern human economy. We ask why both kinds of systems show parallel and accelerating trends toward higher productivity and functional diversity, and why complex ecosystems such as rain forests and coral reefs have persisted for millions of years, whereas human economies since the dawn of civilization seem to have become increasingly unstable and more prone to the destructive effects of monopoly and other disruptions internal to the economy. Finally, we ask whether and how these internal threats might be eased or postponed by regulation and a shift in the criteria for economic success.

Parallel Characteristics and Trends

As they compete for locally scarce commodities, economic agents—individuals, groups, and groups of groups, ranging from humans to firms and nations, from microbes to plants, animals, and animal societies—consume resources and create new ones. These new resources—living and dead organisms, wastes, and new habitats, among many others—allow for still more competition and cooperation. In both natural and human economies, individuals with different abilities join in groups and form mutually beneficial arrangements to compete more effectively with others if their common interest can be adequately defended against cheaters or common enemies. Competition implies differential success in survival and reproduction, leading to selection, which in turn yields and enforces adaptation, a good fit between organism and environment. Adaptation in natural economies is driven largely by natural selection, whereby successful individuals contribute more genes to future generations. In human economies, inheritance is primarily cultural: successful competitors differentially spread knowledge and technology for making a better living and providing resources for their offspring. Competition favors innovation and diversification if the environment—genetic, physiological, and technological—tolerates "experimentation" and errors (Vermeij 2002, 2004*a*, 2009*a*, McShea and Brandon 2010). Through cooperation and accidental mutual benefit, competing agents create and depend on an economic network in which resources are produced, consumed, traded, and recycled. Interdependence and cooperation, in which cheating is suppressed or punished, evolve from interactions among different self-interested agents. In both natural and human economies, cooperation and mutualism are essential for high productivity (the rate of production of usable resources).

The parallels are most evident when ecosystems are compared with the economies of Adam Smith's day, when financial institutions, futures trading, life insurance, and industrial capitalism were still in their infancy (Ferguson 2008). The modern economy, with its instantaneous communication, complex financial transactions, cheap transport, and intricate and wide-ranging cooperative networks, has developed institutions and relationships that have no clear analogs in ecosystems. The underlying processes, however—competition, cooperation, differential propagation of more competitive agents, production, consumption, and trade—operate in all economic systems regardless of their complexity and scale. These processes lead to the same economic trends—innovation, diversification, increased productivity, the emergence of competitive dominants (or centers of authority) among individuals or groups, and increased geographic reach of interaction (Vermeij 2004*a*, 2009*a*).

Competition can lead to innovation. Some innovations enable individuals to escape competition by exploiting new opportunities; others allow economic actors to overcome trade-offs and other constraints by using old resources more effectively; and still others permit agents to collect and interpret more information faster. Economists and evolutionary biologists have noted that an abundant, predictable resource supply coupled with intense competition favors innovations enhancing power, responsiveness, and adaptability, which tend to be costly in time and energy. Novel attributes that enhance competitiveness by increasing power, metabolic performance, mutualism, and energy-intensive means of defense arise in large, productive ecosystems such as forests, grasslands, and reefs, especially in the warm tropics where the range of adaptive possibilities is least constrained by thermal limitations (Vermeij 2004*a*, 2002, Leigh et al. 2009).

Likewise in the human economy, innovations in transport, food production, manufacture, communication, health, education, and the arts are concentrated in situations of agricultural surplus, in parts of the world where at least some individuals, though affected by competition, have access to plentiful natural resources whose availability and use are unencumbered by political instability or totalitarian rule (Smith 1776, Mokyr 1990, Algaze 2001). Prosperity means that wealthy urban dwellers are released from food production to become artisans, priests, traders, teachers, scientists, and entrepreneurs. Productive economies have supported progressively larger cities, which have become centers of innovation and economic activity (Bettencourt and West 2010). All economies develop positive feedbacks among competition, innovation, productivity, and functional diversity. In ecosystems, diversity is expressed as the number of species and their economic roles. Species differ in how they acquire and defend resources; they are producers, consumers, enemies, victims (or food), recyclers, and allies. In human economies, constructed by and for a single species, the formal equivalents of species are occupations (Vermeij 2004*a*). Individuals of different species or occupations interact and cooperate to create an economy.

Positive feedbacks begin when innovation by one agent incidentally creates opportunities or new resources for other agents. In nature, geochemical cycles including those of carbon, nitrogen, oxygen, calcium, phosphorus, silica, and water develop feedback loops in which increasing control by living things over time leads to biochemical innovations for capturing and recycling these essential substances (Fischer 1984, Maliva et al. 1989, Tréguer et al. 1995, Lenton 2001, Berner 2003, Ridgwell and Zeebe 2005, Canfield et al. 2010, Planavsky et al. 2010). Herbivory—the consumption of plant-like organisms—speeds the turnover of nutrients, increasing the system's productivity (Vermeij and Lindberg 2000). Warm-blooded mammals stimulate plant productivity by fertilizing the soil with their wastes (McNaughton 1984). Animals burrowing in sediments on the seafloor release previously unavailable buried nutrients back into the water, where other species exploit them (Thayer 1983). Competition and defense jointly led to the evolution of dense populations and three-dimensionally complex environments—reefs, kelp beds, forests, and grasslands—forming new habitats and spurring economic activity (Vermeij 2004*a*).

In the human realm, as Adam Smith (1776) well understood, innovations such as agriculture, use of fossil fuels for power, factory-based manufacture, and long-distance trade enriched not only those directly engaged in these activities, but also many other members of the economy by spreading wealth and supporting new occupations. These innovations overcame previous limits on the economy's productivity and functional diversity. The Malthusian cap was lifted during the nineteenth century as colonial trade and fossil fuel got the Industrial Revolution underway, creating new products and practices that relieved pressures on European land use and labor (Mokyr 1990, Landes 1998, Pomeranz 2000, Clark 2007). The innovations that made this possible include using productive foreign crops such as potatoes in Europe and wheat in North America, increasing agricultural productivity with artificial fertilizers and pesticides, major advances in medicine, public health, and sanitation, faster public transport powered by engines, and improvements in food storage such as canning and refrigeration. As in ecosystems, however, these innovations also made some livelihoods obsolete and diminished the economic prospects for displaced or exploited workers.

In the same way, the great innovations in the history of life—photosynthesis, aerobic respiration, nitrogen fixation, eukaryotic organization, sexual reproduction, multicellularity, colonization of the dry land, endothermic metabolism, social organization, and symbolic thought (Table 1)—progressively lifted constraints on the scope of adaptation, productivity, diversity, and the scale of activity in ecosystems (Maynard Smith and Szathmary 1995, Vermeij 1999, 2004*a*, Knoll and Bambach 2000). With the evolution of the eukaryotic cell, for example, an estimated 200,000-fold increase in gene expression, made

Table 1. Dates (in Ma, millions of years ago) of major events in the history of life.

Date	Event
3800	Origin of life on Earth
3450	Microbial stromatolites (Allwood et al. 2009)
2700	Oxygenic photosynthesis, microbial ecosystems (Eigenrode and Freeman 2006, Bosak et al. 2009)
2400	Great Oxidation Event (Goldblatt et al. 2006, Blank and Sánchez-Baracaldo 2010)
2100	Eukaryotic cell, colonial organization (El Albani et al. 2010)
2000	Multicellular organization (Bengtson et al. 2007)
1800	Phytoplankton (Butterfield 1997)
1200	Obligate sex, differentiated multicellular organization (Knoll 1992, Butterfield 2000)
1100	Oxidation on land (Johnston et al. 2005, Parnell et al. 2010)
635	Oxygenation, first animals (Fike et al. 2006, McFadden et al. 2008, Shen et al. 2008, Dahl et al. 2010)
550	Mineralized skeletons, burrowing in sediments, zooplankton (Butterfield 2001, Droser and Li 2001, Zhuravlev 2001, Dzik 2005)
500	Ordovician radiation, first terrestrial plants and animals (Masuda and Ezaki 2009, Rubinstein et al. 2010, T. Zhang et al. 2010)
420	Devonian revolution, oxygenation, first charcoal, first active pelagic swimmers (Glasspool and Scott 2010, Dahl et al. 2010, Klug et al. 2010)
300	Expanded terrestrial herbivory and decomposition (Labandeira 2006)
230	Mineralized plankton, endothermy in large animals (Bakker 1980, Falkowski et al. 2004, Vermeij 2008, 2011)
100	Increased photosynthetic capacity, (Boyce et al. 2009, Boyce and Lee 2010, Vermeij 2008, 2011)
30	Grasslands (Retallack 2001)
1	Technological humans

possible by the energy-producing mitochondrial components, took place (Lane and Martin 2010). High productivity made possible by innovations leading to faster resource turnover in increasingly cooperative economic networks thus favored still more energy-intensive information-generating innovations. Economies grow in activity, scale, and interdependence because innovations build upon one another.

Mutualistic endeavor is crucial to the productivity, functional diversity, and emergence of competitive dominants in both human and natural economies. The importance of mutualistic enterprise, much of it founded on trade and trust among strangers near and far, is attested in human economies by the proliferation of laws and sanctions protecting such behavior against cheating, whether it be violating contracts, embezzling, other forms of robbery or violence, perverting justice, or other crimes (Landa 1976, De Soto 2000, Milinski et al. 2002, Seabright 2004, Henrich et al. 2006, 2010, Hauert et al. 2007, Bowles 2008). These codes begin as informal understandings and agreements, but in most large, complex societies they develop as formal regulations, patents, and other legal and ethical rules together with the means to enforce them. The coordinated cooperation enabled by these codes of conduct makes possible tasks that no single individual could accomplish. For example, the manufacture of a poor man's overcoat requires activities ranging from raising sheep, weaving wool, and importing dyes to transporting goods to factories and consumers (Smith 1776). Parents, relatives, friends, book publishers, teachers, architects, and many others must coordinate seamlessly to rear modern children; and numerous skills and occupations are needed to ensure safe and reliable air travel.

In nature, cooperation takes several forms and is variously enforced (Leigh 2010*b*). Some mutualisms, such as that between plants and the ants they feed and house in return for protection against competitors and predators, are enduring associations. Many mutualisms, such as that between animals and vitamin-synthesizing gut bacteria, are self-reinforcing because the symbiont can only reproduce by helping the host. Other hosts acquire live-in symbionts from their surroundings, as when leguminous plants attract rhizobial bacteria to their roots from the soil. In return for safe housing and abundant carbohydrates, these bacteria transform atmospheric nitrogen into fertilizing ammonia, which enhances the host plant's growth. The relationship is enforced by plants denying essential resources to non-performing rhizobia (Kiers et al. 2003, Kiers and Denison 2008). Still other mutualisms involve brief exchanges such as sexual reproduction in promiscuous animals, where mates may never encounter each other again. In such cases, selection favors the evolution of structures or behaviors that attract appropriate and repel inappropriate partners, such as the barriers that prevent fertilization of eggs by sperm from unsatisfactory mates (Darwin 1859, Eberhard 1996).

Three mutualisms illustrate the centrality of cooperation in ecosystems. The first concerns the transformation by natural selection of eubacteria with aerobic respiration parasitizing anaerobic archaebacteria into mutualistic mitochondria. Hosts were better at getting food, whereas the aerobic guests were better at getting energy from that food. There was accordingly a basis for mutualism between host and guest, whereby complementary abilities could be pooled for the common good (Blackstone 1995). Subsequent selection entwined the fates of the mitochondria so closely with that of the host that the mitochondria could only reproduce by helping their hosts (Leigh 2010*b*). This intimate mutualistic partnership—the eukaryotic cell—enabled the evolution of orderly sexual reproduction and provided sufficient energy to support genomes large enough and flexible enough to permit the evolution of multicellular life including algae, fungi, plants, and animals (Lane and Martin 2010).

The second example concerns the mutualism between corals and single-celled photosynthetic algae. The algae provide their hosts' polyps with carbohydrates in return for safety and the nutrient-rich wastes that the corals produce after digesting the planktonic organisms their polyps catch. During the last half-billion years, animal-algal partnerships like this have constructed, and been the dominant competitors for space on, most shallow-water reefs (Jackson 1983, Stanley 2001).

The third example—the pollination mutualism—appeared when understory weeds used flowers to attract animals as pollinators. Mating with the help of animal pollinators allowed plants to maintain genetic variation even when rare enough that most individuals escaped detection by specialized pests. This circumstance allowed plants to divert energy from antiherbivore defense to faster growth (Leigh 1999, 2010*b*). The freedom to grow fast favored the evolution of higher stomatal conductance and photosynthetic capacity (Boyce et al. 2009), which in turn enabled flowering trees to replace slower-growing and better-defended wind-pollinated conifers in all but the least productive habitats (Brodribb and Feild 2010). Although cheating is rife in mutualisms involving pollinators and animal seed-dispersers (Leigh 2010*b*), most tropical plants employ animals for pollination and seed dispersal. Doing so made possible the evolution of flowering rain forest, the most productive and diverse of modern forest ecosystems (Leigh 1999, 2010*b*). Moreover, the fast growth of flowering trees entails copious transpiration. Therefore, flowering rain forest creates its own storms (Corner 1964), greatly expanding the area wet enough to support it (Boyce and Lee 2010).

Mutualisms and other major innovations (Table 1) led to stepwise proliferations of life. Regional and global diversity rose in the sea and even more on dry land (Bambach 1977, Sepkoski et al. 1981, Sahney et al. 2010, Vermeij and Grosberg 2010). The fossil record documents increasing productivity in the sea (Thayer 1983, Kidwell and Brenchley 1996, Droser et al. 2002, Kennedy et al. 2006) and on land (Bambach 1999, Boyce et al. 2009, Knauth and Kennedy 2009); increased metabolic activity in animals (Vermeij 1987, Bambach 1993, Vermeij and Grosberg 2010) and plants (Wilson and Knoll 2010); and increased locomotor speed and distance traveled by animals of all sizes (Vermeij 1987, Vermeij and Grosberg 2010). These developments led to greater interconnection among habitats that were formerly more isolated from each other, such as fresh and salt water, land and sea, the tropics and the temperate zones, and the pelagic realm and the seafloor (Vermeij 2004*a*, 2009*a*). Increased activity, often resulting from mutualistic partnerships and larger-scale interdependence, therefore made natural economies effectively larger over time.

Similar but much faster trends characterize human economic history (Tables 2, 3). They include rising per-capita productivity (output per man-hour), per-capita and collective energy use, consumption of ever more of the world's natural resources (attaining unsustainable levels by 1980), increased agricultural output, proliferation of occupations unrelated to food production, greater exchange of ideas and techniques, and globalization of culture and trade (Cohen 1995, Rojstaczer et al. 2001, Hall et al. 2003, Vermeij 2004*a*, 2009*a*, Brown et al. 2011). These

Table 2. Dates (in Ka, thousands of years before 2000) of major human inventions.

Date	Invention
2500	First tools (Domínguez-Rodrigo et al. 2010)
1900	First cooking (Wrangham et al. 1999)
790	Controlled use of fire (Goren-Inbar et al. 2004)
90	Compound tools, symbolic thought (Powell et al. 2009)
40	Widespread symbolism (Powell et al. 2009)
13	Cultivation of plants (Harris 2003)
10	Domestication-agriculture (Harris 2003)
6.0–5.5	Wheel (Anthony 2007)
5.7	Urbanized society (Algaze 2001)
4.4	First empire (McNeill 1982)
3.1	Iron Age (Mokyr 1990)
2.6	Coins (Ferguson 2008)
2.5	Agricultural wells (Hillel 1990)
1.5	Cutting plow (carruca) (Mokyr 1990)
0.8	Windmill (Mokyr 1990)
0.67	Firearms (McNeill 1982)
0.55	Printing (Mokyr 1990)
0.5	Rise of science (Mokyr 1990)
0.5	Widespread use of coal and peat (Mokyr 1990)
0.5	New World foods spread around the world (Mokyr 1990)
0.3	Use of coke (Mokyr 1990)
0.23	Precision machine tools (Mokyr 1990)
0.2	Industrial Revolution (Mokyr 1990; Clark 2007)
0.16	Artificial fertilizers (Hillel 1990)
0.155	Telegraph (Mokyr 1990)
0.15	Science linked to industry (Mokyr 1990; Landes 1998)
0.14	Widespread use of petroleum (Mokyr 1990)
0.13	Widespread use of electricity (Mokyr 1990)
0.10	Airplane
0.09	Introduction of plastics (Mokyr 1990)
0.05	Nuclear power
0.01	Widespread use of computers

Table 3. Mean time intervals between successive major inventions.

Phase	Time interval	n
History of life (millions of years)		
Phase 1, 3800 to 635 Ma	340 ± 200	9
Phase 2, 635 Ma to present	79 ± 38	8
Human history (thousands of years)		
Phase 1, 2500 to 90 Ka	800	3
Phase 2, 90 to 13 Ka	38.5	2
Phase 3, 13 to 6 Ka	3.5	2
Phase 4, 6 to 0.8 Ka	0.74 ± 0.48	7
Phase 5, 0.8 Ka to present	0.044 ± 0.043	18

trends accelerated rapidly, especially after human beings began five hundred years ago to rely more and more on non-renewable energy sources (Tables 2, 3). The explosive rise in global energy use by humans—an eight-hundred-fold increase in hydrocarbon consumption since 1750 and a twelve-fold rise from 1950 to 2000 (Hall et al. 2003, Brown et al. 2011)—exceeds in both magnitude and speed the three- to four-fold rise in photosynthetic capacity of land plants beginning 100 Ma (Boyce et al. 2009) and the roughly ten-fold increase in metabolic power with the evolution of endothermic vertebrates from ectothermic ancestors beginning 230 Ma (Bakker 1980). In the history of life, perhaps only the emergence of eukaryotic organization rivaled our technological expansion in raising productivity. Using non-renewable resources has at least temporarily offered humanity unprecedented protection against disease and natural predators and allowed it to forge an unsustainable monopoly of Earth's natural resources.

Differences

Compared to natural economies, human economies change much more rapidly (Table 3), and advanced civilizations last much less long (Fisher 1930) and appropriate an ever larger and less sustainable portion of our planet's resources. We propose that the differences in the rates, magnitudes, and scale of these trends and of economic activity between natural and human economies reflect radical contrasts in the modes of origin and transmission of adaptations. In nature, most adaptations come to be specified and regulated by genes, which are usually transmitted vertically from parent to offspring. The genomes of eukaryotes are organized to ensure that recombination during meiosis, the process by which the offspring receives one version (allele) of a gene at each position in the genome from each parent, allows alleles and their effects to be tested in many genomes. Alleles therefore spread according to how they improve their bearers' competitiveness rather than their ability to bias meiosis in their own favor or the merits of the particular genome in which they first arose (Fisher 1930, Felsenstein 1974, Leigh 2010*a*). Among prokaryotes such as bacteria, genes often pass horizontally from one individual to another unrelated one, and can occasionally even pass to eukaryotes. Horizontal transmission of genes created a genetic community of prokaryotes in which evolution was primarily at the biochemical rather than the morphological and behavioral level and in which biochemical achievements far surpassed those of eukaryotes (Woese 1998, Vetsigian et al. 2006, Doolittle and Bapteste

2007). It also accounts for the rapidity with which bacteria exchange genes and generate new combinations to adapt to new conditions, including the antibiotics humans have deployed against them. On the other hand, horizontal transmission often allows genes alone or in groups to spread like a disease without regard for the good of their hosts. Excluding horizontal transmission of genes allowed the evolution of large multicellular organisms.

Non-genetic influences on physiology, behavior, and form are common in nature. Many animals with keen powers of observation and a capacity for rapid response learn from or copy others' behavior, and thus exemplify a form of cultural transmission of adaptations among neighbors. Many adaptations originate as environmental plasticity (direct effects of the environment on expression of traits) and only later become genetically determined (Newman and Müller 2001, Peterson et al. 2009). At the ecosystem level, species regularly invade new habitats and regions (Vermeij 2005). These cases notwithstanding, genetic adaptation remains the predominant norm in natural economies.

By contrast, adaptation in the human economy is by the horizontal and vertical spread of ideas, knowledge, and technology, as expressed in symbols such as spoken or written language, so that adaptation is much faster and affects people and their economies on a much larger scale. Cultural transmission of adaptation has propelled humanity to its current status as the dominant economic agent on Earth. Although the cultural basis of adaptation is enabled by gene-based evolution of the brain and associated sensory and motor systems, rapid long-distance communication allows inadequately tested or overtly harmful ideas to spread like epidemic diseases without regard to their ultimate benefit either to their carriers or to the economy as a whole.

The overwhelmingly cultural nature of adaptation in human economies shifted the primary sources of economic collapse from external causes to more internally generated ones. Potential threats fall into three categories: (1) external disruptions, especially those that interfere with the primary production on which the economy's members depend; (2) tragedies of the commons, where each individual benefits from increased exploitation of a resource on which all members of the community depend but where increased collective exploitation ruins the resource for all (Hardin 1968, Milinski et al. 2002, Penn 2003); and (3) monopolies, in which an exceptionally powerful agent emerges to control resources and economic activity while suppressing competition and thwarting the more efficient use of resources (Smith 1776).

External disruptions nearly always harm economies because these systems and their members are well adapted to their circumstances (Leigh 1999). The mass extinctions of the geological past have various external causes—vast volcanic episodes, collisions between Earth and celestial bodies, and their climatic consequences—but all stem from global disruptions to primary production and to the major biogeochemical cycles (Berner 2003, Vermeij 2004*b*, Ridgwell and Zeebe 2005). These disruptions also threaten top consumers, whose high metabolic demands cannot be met when a copious, predictable food supply is interrupted (Vermeij 2004*b*). Most major transformations in the composition of dominant members of reefs, level-bottom marine ecosystems, forest vegetations, guilds of herbivores and predators, and the plankton coincide with mass extinctions, and are characterized by gaps of hundreds of thousands to as much as ten million years between the last appearance of the old guard and the emergence of the new hegemony (Bakker 1980, Boucot 1983, Benton 1983, Niklas 1986, Stanley 2001), where the emerging dominants come from the ranks of fecund but competitively subordinate ancestors (Vermeij 2004*b*).

The tendency for human economies to expand as far as resource availability allows renders them susceptible to external disruptions such as climate change. Indeed, many human societies, such as the Anasazi of the American Southwest and the Norsemen of medieval Greenland, declined during prolonged spells of adverse climate when productivity decreased and the available resources could no longer support them (Diamond 2005). In China, major political, social, and economic upheavals statistically coincide with climatic fluctuations (P. Zhang et al. 2008). Modern societies are more closely interconnected, enabling local economies to survive disasters that would formerly have devastated them. On the other hand, advanced technology and the copious use of wood and fossil fuel have enabled humanity to escape regulation by disease and large predators, with the result that humans exploit a huge fraction of Earth's diminishing resources (Lamb 1982, Perlin 1989, Jackson et al. 2001, Worm et al. 2006). The global human economy is accordingly more vulnerable to environmental change, much of which is of our own making.

A central threat to both human and natural economies is posed by tragedies of the commons, where the pursuit of self-interest by each individual reduces access to a resource on which all members of the community depend (Hardin 1968). Familiar examples in the human realm include reduced productivity stemming from the release of greenhouse gases like carbon dioxide through the burning of fossil fuels, leading to global warming and to acidification of ocean waters (Hall et al. 2003, Ridgwell and Zeebe 2005, Kump et al. 2009); the overexploitation of forests and fisheries (Perlin 1989, Jackson et al. 2001, Worm et al. 2006, Rustagi et al. 2010); the spread of unproductive, oxygen-deficient zones in coastal marine waters thanks to agricultural and urban runoff rich in biologically available nitrogen (Diaz and Rosenberg 2008) and perhaps also to removal of consumers (Vermeij 2009*b*); and overgrazing of communally held pasture by self-interested pastoralists (Hardin 1968). In all these cases, immediate self-interest conflicts with the common good, and leads to harmful, often unintended consequences whose costs are either exported or borne by the economy as a whole rather by the perpetrators.

Beginning with the Dutch tulip mania in the seventeenth century but greatly expanding in the twentieth, complex financial relationships with no analogs in ecosystems allowed collective delusions, which are spread by wealth-seeking banks, investors, and speculators, to destabilize the human economy from within (Chancellor 1999, Ferguson 2008, Haldane and May 2011). The myth that stock prices would rise disproportionately to income forever and ever contributed to the Great Depression. The financial crisis of 2007–2008 was precipitated when financial instruments that put a price on future risk failed to yield hoped-for profits for some very large, highly connected banks, sending shock waves throughout the financial markets. Together with the fiction that house prices would continue to rise relative to income and that people with insufficient income could continue to pay off inadequately secured mortgages, these delusions spread throughout much of the world economy, causing overall instability and a crisis of confidence. For a time, the system provided the credit that allowed the economy to grow, fueling the fiction that economies can expand without limit; but this debt-based growth was unsustainable. The meteoric twentieth-century rise in advertising, which tilts the supply-and-demand marketplace heavily in favor of large retailers and producers (Slawson 1981) and whose effectiveness has been vastly magnified by mass communication, has been instrumental in propounding these delusions and creating unrealistic economic wants and expectations. Propaganda and falsehoods likewise spread unchecked around the world, giving life to ideologies that conflict with evidence-based, much more thoroughly tested ways of knowing.

Warfare—a form of intergroup competition with very ancient human cultural roots (Bowles 2009)—is another chiefly human internal threat that diverts a significant fraction of wealthy nations' resources from more productive ends (Nincic 1982, Russett 1983). Although the cooperative behavior of self-interested individuals is enhanced and perhaps even culturally fixed by warfare (Bowles 2009, Darwin 1859, Crofoot and Wrangham 2010), armed human conflict has become exponentially more destructive to human and natural economies alike as the weapons escalation among nations continues. Violence in general and warfare in particular have claimed smaller percentages of the human population over the course of history (LeBlanc 2003, Clark 2007), but there has been an enormous rise in power of individual weapons—by ten orders of magnitude from the mid-nineteenth to the mid-twentieth century alone, from the equivalent of 10^{-3} to 10^{7} tons of TNT—magnifying the threat of global catastrophe. These increases vastly exceed the approximately ten-fold increase in the bite force of the most powerful marine predator over the last 300 million years or the three- to four-fold rise in photosynthetic capacity of land plants over the last 100 million years (Vermeij 2004*a*, Boyce et al. 2009).

Ecosystems have also faced, and often overcome, internal threats. Molecular oxygen liberated by Cyanobacteria beginning about 2.7 billion years ago was a potent toxin for contemporary life-forms before the respiratory pathway evolved to use oxygen as an electron acceptor (Vermeij 2004*a*). Land plants gain a competitive advantage by placing their leaves above their neighbors' to secure access to light, compelling neighbors to do likewise. The result is a tall forest, in which trees devote almost as much energy to growing wood to support leaves in the canopy as to grow the leaves themselves (Leigh 2008). In the early history of forests, vast amounts of dead plant material accumulated in the soil, where it was largely unavailable to the trees. The burial of this material, which escaped oxygenation, led to higher oxygen and lower carbon dioxide levels in the atmosphere, reducing photosynthetic efficiency (Beerling and Berner 2005). These effects were partly reversed first by the evolution of large decomposers, which recycled much of the organic matter back into the forest, and later (around 300 Ma) by a major increase in herbivory, which stimulated plant productivity by favoring faster plant growth (Robinson 1990, Labandeira 2006). The tragedy of forest wood-making was resolved in dry climates when, beginning about 30 Ma, large mammals knocked over forest trees to eat their leaves, allowing the spread of grassland, a low-growing vegetation maintained and made more productive by large grazing mammals (Leigh et al. 2007, Leigh 2008, 2010*b*).

In general, resolution of tragedies of the commons in nature occurs only when the primary criteria for competitive success, such as plant height or mode of defense, are replaced by new criteria. These changes occur as the result of innovation, often in the pattern of consumption or by the addition of feedback loops that enhance resource recycling. Although these effects are incidental consequences of adaptive evolution in third parties not directly engaged in the competitive races that yield the tragedies of the commons in the first place, their great importance lies in changing the rules of the competitive environment for dominant economic agents.

Monopoly, another internal economic threat, results from the emergence of overwhelmingly powerful agents—usually groups of well-organized coalitions—that reduce the efficiency of resource use by suppressing competition. Such monopolies pervade the modern human economy but were rare, local, and temporary in natural economies until cultural transmission of knowledge and technology became the dominant agency of change in our species. In the modern economy, corporate and state monopolies exclude even those competitors that can exploit the monopolized resource more effectively, thereby diminishing opportunities to solve problems arising from tragedies of the commons and distorting the relationship between supply and demand (Smith 1776). In addition, monopolies concentrate control in such a way that harmful actions and decisions are not easily corrected, because no other economic actors are powerful enough to take countermeasures or even to detect the error (Vermeij 2009*a*).

The rarity of monopolies in nature reflects the limited power and reach of dominant economic agents. One example of a natural monopoly is upland forest hectares dominated by a single tree (*Tococa occidentalis*), which houses vicious ants that protect the tree against herbivores and encroaching vegetation (Morawetz et al. 1992). The trees use light much less efficiently and cause more soil erosion than normal pioneer trees that house ants. *Tococa* trees die and the monopoly ends when crowns of nearby canopy trees beyond their ants' reach expand into the clearing in which *Tococa* grows (Morawetz et al. 1992). The monopoly thus remains small-scale and disappears within a few years.

The evolution of modern *Homo sapiens* represents the first instance in the history of life of the emergence of global monopoly by a single species in a natural ecosystem (Vitousek et al. 1997, Vermeij 2009*a*). This status was achieved largely through technology that extends beyond the living body and that allows our species to exploit previously untapped sources of energy. This evolution has been so rapid and has led to such high per-capita and collective rates of energy metabolism that the human species has come to overshoot the productive and regenerative capacity of the whole biosphere. As a result, ecosystems from which potential competitors could invade to restore the balance of power no longer exist, because none is beyond the reach of the human monopoly. In short, the economic

Table 4. Summary of comparisons between natural and human economies.

Comparison
Similarities and parallels
The system is adaptive
Members compete for locally limiting resources
Resources are produced, consumed, traded, and recycled in a cooperative network
Competition favors innovation under permissive conditions
Positive feedbacks exist among competition, innovation, productivity, and diversity (number of species or occupations)
Productivity increases over time
Diversity increases over time
Successively more powerful top competitors (individuals, groups, and mutualisms) emerge over time
The scale of economic activity increases over time
Trends accelerate over time
Differences
Origin and transmission of adaptation: genetic in nature, cultural in human economies
Rates, magnitudes, and scale of economic activity and adaptation: much greater in human economies
Trends: much faster in the human economy
Threats
External disruptions leading to collapse in primary production: predominant threat in natural and early human ecosystems
Internally generated tragedies of the commons: common in both systems
Internally generated monopolies: rare in nature, common in human economy

activities of our species have for the first time in the history of life exceeded the resilience and robustness of ecosystems, effects that only external disruptions to production were able to bring about in earlier geological periods.

Conclusions and Prospects

The origin of human monopoly coincides with the rise to predominance of cultural over genetic adaptation. As manifestations of that profound shift, cooperation and the formation and cohesion of groups as powerful economic agents have become cultural and technological. Human monopoly strengthened when humanity turned to fossil fuels as sources of energy. As a result, the modern human economy is increasingly being threatened and destabilized by internal, horizontally propagated financial and political delusions and by the elimination of agencies that could have capped our exploitation of natural resources.

The similarities and differences between natural and human economies that we identify, summarized in Table 4, indicate to us that ecosystems owe their robustness and resilience to adaptive accommodation. It is particularly striking that natural economies can absorb considerable change, including the arrival of new species and the replacement of others, by effective regulation, often imposed by top consumers and producers. Such regulation prevents the overexploitation of resources (Hairston et al. 1960) and, more speculatively, creates a modular economic organization in which tragedies of the commons and monopolies do not spread through or destabilize the system as a whole (Roopnarine et al. 2007, Haldane and May 2011). We note, for example, that the destruction of low-diversity forests by pine bark beetles and spruce budworm in North America is taking place in the absence of formerly abundant top predators, which kept trees healthy by limiting large herbivores. The well-documented depletion of minerals from forest soils in Alaska, Sweden, Australia, New Zealand, and the Hawaiian Islands, leading to dwarfing of the vegetation (Wardle et al. 2004), affects forests from which top herbivores and predators have become extinct without equivalent replacement (Vermeij 2009*b*). The worldwide spread of coral diseases on reefs and of toxic red tides could be due to overfishing of large predatory and herbivorous species. In all these cases, ecosystems have become more vulnerable to internally generated disruptions because of the loss of effective evolutionary regulation and the erosion of modular organization.

In the modern globalized human economy, it is no longer possible either to externalize the costs of economic activity, manifested in the many tragedies of the commons we face, or to limit the power of our species by conventional means. Our collective monopoly of the biosphere is likely to be constrained only through the destructive effects of shortages of food and fuel or by the imposition of external calamities, all of which will precipitate mass disruption and suffering. Taking a cue from the history of natural economies, we suggest that the long-term health of the human economy and that of the biosphere as a whole, insofar as it is achievable, will require substantial preemptive regulation together with fundamental changes in the criteria by which human-economic success of individuals and societies are measured. A major and urgent political challenge is therefore to identify and implement the cultural adaptations to contain the internally generated agencies that threaten to overwhelm us and the ecosystems on which we depend.

It will be necessary for humanity to regulate economic activity. In an economy that already consumes fuels and other resources unsustainably, regulation must limit resource use through mechanisms such as taxation, debt ceilings, reducing the huge and growing inequality of income among and within countries, restricting financial and land speculation, incorporating environmental costs in prices, protecting the means of production in ecosystems, and punishing cheaters consistently and effectively. In nature and in growing human economies, regulation developed through adaptation and the mutual accommodation of multiple agents. This development somewhat resembles Adam Smith's (1776) "invisible hand" in an idealized "free market." Over time, however, even in growing economies, the actions and policies of powerful governments, corporations, and international agencies came to dominate the market in the same way that the actions of many animals are centrally orchestrated in the brain. The "invisible hand" loses its grip because the "free market" is poorly equipped to cope with global tragedies of the commons and the shortages of commodities for which there are no adequate substitutes. The regulation required to overcome these effects must remain flexible enough to test competing solutions and must preserve incentives among competing self-interested parties as much as possible (Penn 2003).

The likelihood that such "voluntary" limitation of economic activity through regulation can work or even be implemented is small. In the history of life as well as in human political history, powerful entities do not willingly cede power without threats from other parties or from externally imposed catastrophe. Moreover, economic polices the world over favor rapid economic growth even though such growth cannot be sustained in the long run. Ideologies denying evolution, global warming, economic limitation, and overpopulation are deeply entrenched and stand in the way of recognizing problems or considering potential solutions. Still, if we could slow growth or stabilize our economic imprint, we would gain much-needed time to identify and establish suitable strategies for managing declining energy supplies and addressing ourselves to the many global tragedies of the commons that humans and the rest of life on Earth face.

Besides the necessity for regulation, the long-term health of the intertwined human and natural economies will require a shift in what Ehrlich and Levin (2005) call societal norms. In the same way that natural tragedies of the commons have been lessened or eliminated by innovations and adaptations that changed the criteria of success in competition, the internal economic disruptions for which humans are responsible cannot be undone without a change in how we measure social and economic standing. Our species must work toward a greater separation between competitive performance, as reflected in individual and group status, and material wealth. Such a transition will require greater emphasis in our ethical values on a sense of mutual responsibility that extends beyond human well-being and group allegiance to protection of the Earth as a whole. Trends in advanced capitalist societies toward philanthropy, in which high-status economic players redistribute much of their wealth to projects in the broader public's and biosphere's interest, and toward greater public spending by governments on social programs that reduce economic inequalities (Lindert 2004) represent hopeful first steps in this cultural transformation.

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