Human Footprints in the Ecological Landscape

P. G. FALKOWSKI and D. TCHERNOV

Environmental Biophysics and Molecular Ecology Program, Institute of Marine and Coastal Science, Department of Geological Sciences, Rutgers, State University of New Jersey, New Brunswick, NJ 08901, U.S.A.

> "O Oysters," said the Carpenter, "You've had a pleasant run! Shall we be trotting home again?" But answer came there none — And this was scarcely odd, because They'd eaten every one.

Through the Looking-Glass and What Alice Found There by Lewis Carroll (1872)

ABSTRACT

In this chapter we explore how the evolution of human behavior has led to the current condition, the quantitative impact of humans on ecological and biogeochemical processes, and potential strategies for developing a sustainable partnership between humans and the ecosystems in which they operate. Our basic thesis is that humans appear to have uniquely escaped from the Red Queen constraint of adaptive genetic selection. The subsequent consequences of that escape has led to rapid alterations of all ecosystems on Earth. The alterations were so rapid and so strong that they exerted selection pressures not unlike a mass extinction event.

INTRODUCTION

Human Evolution

The complete sequencing of the human genome has facilitated detailed molecular reconstructions of the evolution of *Homo sapiens*. A recent phylogenetic analysis suggests that our species arose approximately 200,000 years ago and is descended from a closely related, deeply rooted, but extinct species in the same genus (Figure 11.1), which itself arose approximately 5 million years (Ma) from another, extinct, primate lineage (Carroll 2003). The molecular reconstruction, in conjunction with incomplete physical anthropological evidence, indicates

that for almost all of human history, subsistence was based on small nomadic groups cooperatively engaged in hunting and gathering. It is likely that these groups were closely related through family ties. Regardless, aided by geographic dispersion, restrictions in gene flow gave rise to several genetic clades or subpopulations, which can be identified by maternally inherited (i.e., non-Mendelian) information retained in mitochondrial genomes (Sykes 2001). Although genetic differences among individuals within subpopulations can be large, all human subpopulations remain capable of interbreeding. Competition between subpopulations has often led to violent outcomes and even extinction of some.



Figure 11.1 The evolutionary tree for humans adapted from Carroll (2003).

In the twentieth century of the common era, the ensemble of the subpopulations within the subpopulations comprising *H. sapiens* rapidly expanded. Over a period of 100 years, the population grew from ca. 950 million to more than 6000 million. This unprecedented rate of expansion in population paralleled an unprecedented strain on Earth's natural resources. Humans presently consume or exploit ca. 42% of the terrestrial net primary production (Vitousek et al. 1997). Our species has displaced, extinguished, or impacted virtually every extant vertebrate species (Jackson et al. 2001). With very few exceptions, humans have altered the flow and chemical form of all naturally occurring elements as well as all of the fresh water on the planet (Falkowski et al. 2000) (Table 11.1, Figure 11.2). These activities, which further require inputs of energy, are claimed for the food, fiber, and habitat of a single species. The continued growth of human

| Element | Flux | Magnitude of flux (millions of metric tons per year) | | Change due to human |
|----------------------------------|---|---|---------------------|---------------------|
| | | Natural | Anthropogenic | activities (%) |
| С | Terrestrial respiration and decay CO₂ Fossil-fuel and land-use CO₂ | 61,000 | 8,000 | +13 |
| Ν | Natural biological fixation Fixation owing to rice cultivation, combus- tion of fossil fuels, and production of fertilizer | 130 | 140 | +108 |
| Р | Chemical weatheringMining | 3 | 12 | +400 |
| S | Natural emissions to atmosphere at Earth's surface Fossil-fuel and biomass-burning emissions | 80 | 90 | +113 |
| O and H (as H ₂ O) | Precipitation over land Global water usage | 111×10^{12} | 18×10^{12} | +16 |
| Sediments | Long-term prein- dustrial river sus- pended load Modern river suspended load | 1×10^{10} | 2×10^{10} | +200 |

Table 11.1 Examples of human intervention in the global biogeochemical cycles ofcarbon, nitrogen, phosphorus, sulfur, water, and sediments. Data are for the mid-1900s(Falkowski et al. 2000).



Figure 11.2 Changes in human population and atmospheric inventories of CO_2 , N_2O , and CH_4 over the past 2000 years.

population through at least the first half of the twenty-first century will undoubtedly force an even greater exploitation of resources, with an inevitable increase in the human footprint on the ecological landscape. Clearly, such a condition is not sustainable, yet an off-ramp is not clearly visible in the trajectory of human domination of Earth's ecosystems.

SUSTAINABILITY

The concept of sustainability is frequently invoked but there is no consensus on a commonly accepted definition. We opt to define sustainability as a domain in space–time on a planet where the local time rate of change (i.e., the first derivative with respect to time) for all resources used by all organisms in the ecosystem is zero. This domain is not static. It changes with externally forced variables such as climate, tectonic activity, and planetary evolution in the broadest sense. On Earth these processes are ultimately linked to solar radiative output and the Earth's radiogenic heat flux. On long geological timescales, these processes change, yet Earth has remained habitable for over 3500 Ma out of the ca. 4600 Ma of its existence. Although sustainability on any planet is impossible on infinite timescales, it is clearly achievable for a relatively long period (Knoll 2003). Such sustainability must, therefore, be driven by internal feedbacks in biological processes that can adjust the output of metabolic processes to constrain broadly atmospheric gas composition and energy flow for long periods (Lovelock 1979).

On a planetary scale, the chemistry of life involves sets of redox couples that are constrained by feedbacks (Nealson and Conrad 1999). The evolution of the

feedbacks is itself not haphazard, yet we do not understand if there is a unique solution or there are multiple solutions that permit life to persist continuously as long as the planet remains within a zone of habitability (Kasting et al. 1988). The major metabolic sequences on Earth evolved over a period of ca. 2000 Ma and are based on coupled redox reactions that are far from thermodynamic equilibrium (Falkowski 2001). All organisms mediate phase-state transitions that add and remove gases from the atmosphere, and add to and remove solids from the lithosphere. For example, autotrophic carbon fixation converts gaseous CO₂ to a wide variety of organic carbon molecules, virtually all of which are solid or dissolved solids at physiological temperatures. Respiration accomplishes the reverse. Nitrogen fixation converts gaseous N2 to ammonium and thence to organic molecules, whereas denitrification accomplishes the reverse. Calcification converts dissolved inorganic carbon and Ca to solid phase calcite and aragonite, whereas silicification converts soluble silicic acid to solid hydrated amorphous opal. Each of these biologically catalyzed processes is dependent upon specific metabolic sequences (i.e., gene families encoding a suite of enzymes) that evolved over hundreds of millions of years of Earth's history, and have, over corresponding periods, led to the massive accumulation of oxygen in Earth's atmosphere, and carbonate and organic matter in the lithosphere. Presumably, because of parallel evolution and lateral gene transfer, these metabolic sequences have frequently coevolved in several groups of organisms that, more often than not, are not closely related from a phylogenetic standpoint (Falkowski 1997). Based on their biogeochemical metabolism, these homologous sets of organisms are called functional groups or biogeochemical guilds, that is, organisms that are related through common biogeochemical processes rather than a common evolutionary ancestor.

Although functional groups form paired reaction pathways, their evolution was not initially so straightforward. The initial tempo of evolution of functional groups was almost certainly dictated to first order by selection based on redox gradients. Hence, depletion or production of substrates or products almost invariably leads to metabolic innovation, which couples the gradient through energy extraction or production. On Earth, the photobiological oxidation of water and subsequent oxidation of Earth's atmosphere liberated both the carbon reducers (oxygenic photoautotrophs) and carbon oxidizers (heterotrophs) from local electron sources and sinks, and thereby facilitated a pathway that ultimately led to colonization of land. However, although the innovation of water splitting altered the biogeochemical landscape of Earth forever after, the rate of evolution of that process has been extremely slow. All oxygenic photoautotrophs utilize a set of proteins that incorporate a Mn tetramer and pyrite-derived FeS clusters (Blankenship 2001). The evolutionary divergence of these proteins is extremely small, yet the biochemical turnover of the proteins is extremely fast. On average, all reaction centers in photoautotrophs are degraded and replaced every 30 minutes (Prasil et al. 1992), yet selection has not resulted in a solution

to this seemingly incredible inefficiency. Similarly, nitrogen fixation, which evolved from a single common ancestral metabolic suite prior to the oxidation of Earth, remains an anaerobic process. In cyanobacteria, half of the nitrogenase appears to be inactivated by molecular oxygen at any moment in time. Although elaborate, and sometimes incredible, metabolic and structural innovations have evolved to protect the enzyme from oxidative damage, the core machinery has remained fundamentally unchanged (Berman-Frank et al. 2001).

Our point here is that the *realized* tempo of evolution of key metabolic pathways which characterize functional biogeochemical groups is very slow. Metabolic innovation was accomplished in the first 2500 Ma of Earth's history in microbes. In the succeeding 2100 Ma, *life-forms* changed, but *metabolic sequences* remained relatively unaltered. The changes in life-forms were driven by changes in substrate supplies and ecological opportunities. For example, in the oceans, there are eight divisions of eukaryotic oxygenic photoautotrophs comprised of 20,000 species. All these organisms obtained their metabolic machinery by pirating and enslaving a common cyanobacterial ancestral plastid (Delwiche 1999). Virtually no innovation occurred in this process; the host cells evolved specialized armor or nutrient acquisition strategies that facilitated ecological success, but even many of these processes were appropriated from prior evolutionary experimentation in prokaryotes.

The last grand experimentation in Earth's history occurred in the Paleozoic, with the invention of lignin. The rise of terrestrial plants and their rapid colonization of land resulted in resource plunder and may have accelerated weathering reactions that led to a decline in CO_2 and a (poorly documented) rise in O_2 (Berner et al. 2000). Feedbacks, driven by N_2 fixation as well as perhaps combustion, set Earth's O_2 concentration within narrow bounds (Lenton and Watson 2000; Falkowski 2002).

For the past 210 Ma, the carbonate isotope record shows an overall 1.5% increase in ¹³C, suggesting a net burial of only 3000 Gt of organic C and an overall increase in O₂ of ca. 0.3%. Hence, despite several ocean anoxic events in the Cretaceous, the K/T extinction, and the Paleocene thermal maximum 55 Ma, from a biogeochemical perspective, the biologically mediated fluxes of gases and solids to Earth's atmosphere and lithosphere have been, to first order, close to steady state. Over this same period, however, it appears that a long-term depletion of CO₂ occurred and was accompanied by an increase in diversity of both photoautotrophs and aerobic metazoan heterotrophs (Rothman 2001). Changes in supply of substrates have been offset by changes in demands by consumers; the Earth system has been largely in the phase space we defined as sustained; however, one critical substrate, CO₂, has become increasingly scarce. In fact, over the past 15 Ma, the paucity of CO₂ is written in the carbonates, not by an increase in δ^{13} C but by a decrease. This apparently counterintuitive phenomenon reflects the invention and radiation of C4 photosynthesis, where the core metabolic machinery of oxygenic photosynthesis is preserved but several previously *invented* anapleurotic enzymes were summoned to extract CO_2 from an increasingly depleted pool — and to increase the supply of the substrate to the core machinery (Sage 1995). In so doing, the organic matter buried became isotopically heavier whereas the total amount buried barely changed. On the scale of biological innovation, the evolution of C4 plants was more akin to the transition from Baroque to Classical music than from Baroque to Hip Hop.

Although such innovations were small, they occurred on relatively long timescales compared with human evolution. For example, the evolution of C4 plants was itself a continuation of the evolution of photoautotrophs throughout the Cenozoic. Following the K/T extinction, the radiation of browsing mammals helped denude continental plateaus, which led to the evolution and radiation of (C3) grasses. The rise of grasses, which originated around the late Paleocene thermal maximum, was further accelerated by the evolution of grazing mammals, such as ungulates and horses. This feedback cycle accelerated silicon weathering (Conley 2002; Falkowski et al. 2003).

Grasses contain 6-10% dry weight of silicon (Epstein 1994). The deep roots of these organisms not only extract silicon from continental regolith but repackage the element in a form that is much more soluble. Natural burning of grasslands, rain on dead grass, and the mobilization of minerals in fecal material increased silicon fluxes to the coastal oceans and promoted a dramatic radiation of diatoms from the Eocene to present. Diatoms are the most efficient exporters of organic matter to marine sediments. The rise of diatoms appears to have further increased the drawdown of CO₂ and, by the Miocene, led to the rise of C4 grasses (Hayes et al. 1999). We suggest that these interconnected marine and terrestrial functional groups, connected by silicon, coevolved because of CO₂ depletion throughout the Cenozoic. The tempo of evolution is written in the genomic patterns of diatoms, grasses, and ungulates. Coevolution occurred through natural selection and while many species appeared and went extinct over this time, the overall biogeochemical pattern approached a sustainable condition because the time rate of change in the geochemical processes was slow or slower than the rates of evolutionary selection.

THE RED QUEEN HYPOTHESIS

The idea that coevolution increases stability by maintaining a constant rate of extinction and radiation over millions of years is called the Red Queen hypothesis (van Valen 1973). The gist of the idea is that, in tightly coevolved interactions, evolutionary change by one species (e.g., a prey or host) could lead to the extinction of other species (e.g., a predator or parasite), and that the probability of such changes might be reasonably independent of species' age. This idea, named after Lewis Carroll's character in Alice in Wonderland, proposes that evolution within a species must keep pace with environmental selection or the species will go extinct. In other words, each extant species has to "run" to stay in

place. It is a useful heuristic device — which may or may not be correct — but serves as a starting point to examine how human evolution diverged from other species that inhabit Earth.

HUMAN ESCAPE FROM THE RED QUEEN

The evolution of *H. sapiens* rapidly changed Earth. Two major attributes of humans distinguish us from all other organisms (Table 11.2). These attributes have allowed humans to dominate the terrestrial landscape, but not without ecological costs, many of which are not yet recorded in the ledger of natural history.

A distinguishing feature of human evolution is clearly the evolution of complex language (Lieberman 2000). Human language permits communication of abstract thoughts through oral, visual, and written media. In the modern epoch, our communication skills are so honed that we can transfer, virtually instantaneously, vast bodies of knowledge across generational and geographic boundaries without changing a single gene within our gametes. Whereas other organisms, especially vertebrates, have limited communications skills, the quantum evolution that led to the extraordinary development of such attributes in *H. sapiens* appears unprecedented in the history of the planet. Language gave humans an incredible capacity to accommodate rapidly to, and indeed affect, the environment in ways no other organisms can.

The second attribute is the ability to create advanced tools. In this capacity, humans have excelled not only in fabricating instruments to acquire food and build shelters more efficiently — processes that clearly have parallels in other organisms — but in also altering natural materials to produce substances that otherwise never would have been found in nature. The examples of such massive alterations of materials are so enormous and so obvious to most of us that we tend to overlook their importance.

The result of the evolution of language and the ability to create advanced tools is, however, more subtle and dangerous. These two traits have permitted,

| Body shape and thorax | Elongated thumb and shortened fingers | | |
|--|---------------------------------------|--|--|
| Cranial properties (brain case and face) | Dimensions of the pelvis | | |
| Relative brain size | Presence of a chin | | |
| Relative limb length | S-shaped spine | | |
| Long ontogeny and lifespan | Language | | |
| Small canine teeth | Advanced tool making | | |
| Skull balanced upright on vertebral column | Brain topology | | |
| Reduced hair cover | Economic structure | | |

Table 11.2Selected traits that distinguish humans from other apes (adapted from
Carroll 2003).

and ultimately perhaps even required, a new form of knowledge, which we will call *distributed knowledge*. If we consider what each of us *individually* knows or knows how to do, we are hard pressed to recreate the world most of us know. For example, someone, somewhere knows how to make a light bulb, but very few of us individually have that knowledge. Moreover, we no longer go to a professional light-bulb maker and contract with him or her to make some specific light bulbs for us. Rather, a community of people has made machines that make and shape the glass for the bulbs, extracts, purifies, and fashions the tungsten elements, makes the metal base, pulls the vacuum during the manufacture, etc. Light bulbs are now made anonymously by groups of individuals, working with machines, made by other groups of people, each with specific individual knowledge. The knowledge is distributed.

The ensemble of human knowledge and skills is transmitted across geographical boundaries without need for genetic alteration. In so doing, skills are traded to create an *economy*. We assert that a fundamental *emergent property* of the evolution of speech and tool making is economic structure — a phenomenon unique to human society.

THE EVOLUTION OF CONSCIENCE AND SOCIAL BEHAVIOR IN HUMAN SOCIETY

One hallmark of human evolution is the concept of the distant future. Whereas experiential knowledge in many animals leads to both conditioned and learned behavior, anticipation of the distant future in humans is often intense. On an individual level, it can lead to anxiety, depression, or suicide. On a social level it can lead to war between subpopulations.

The ultimate anticipation in an individual's life is the concept of one's own inevitable mortality. The human fascination with death, the dead, and rituals surrounding mortality has led to many unique facets of human behavior, of which the emergence of irrational belief structures is but one of many manifestations (Becker 1997). Another facet is the striving to accumulate "wealth." Although it may be obvious that dogs do not pray (at least en masse), neither do they tend to hoard material resources.

The accumulation of "wealth" (an outcome of distributed knowledge and the evolution of economies) is not unique to humans, but the manifestation of "wealth" with regard to the amount of resources that can be acquired per individual human obeys no simple natural rules. The motivation is, however, usually quite obvious. Accumulation of wealth within a genetic lineage helps to ensure success of future generations regardless of physical or mental abilities (i.e., "skills"). Although humans without wealth have higher rates of fecundity, they also have higher rates of mortality. In human societies, wealth confers a greater probability of reproductive success among individuals who are physically or mentally deficient. Aided by tools in the contemporary epoch, otherwise

infertile but wealthy human couples can even produce offspring by external fertilization.

Wealth is not a concept unique to humans — dogs bury bones and squirrels hoard nuts. However, dogs and squirrels do not use bones and nuts as a vehicle to entice other dogs and squirrels to build warmer and larger dog and squirrel houses, let alone breed more squirrels and dogs via external fertilization. The accumulation of wealth is understandable in a biological context as a form of competition; competition between humans and other species (e.g., for habitat), between subpopulations of humans (for material resources as well as habitat), and between individuals within the same subpopulations (e.g., for mates).

The anticipation of death and the accumulation of wealth within societies have been two forces motivating a second form of knowledge, which, for want of a better term, we will call *ethical knowledge*. Ethical knowledge is a code of conduct that is culturally derived, but transcends cultures. It provides a basis, not unlike game theory, for dynamic competition within subpopulations with clear biological outcomes. Over the course of human evolution, a sentimentalization of human life emerged, such that ethical knowledge forced increasingly altruistic behavior, ultimately leading to long-term desires to extend human life expectancy and decrease mortality. These desires, combined with language and tool-making capabilities, have greatly and increasingly led to resource plunder over the past several hundred years of human evolution.

INCREASING COMPLEXITY MAGNIFIES THE DEMAND FOR NEGENTROPY AND ENERGY

Although humans may (at least temporarily) escape the Red Queen constraints, no organism can escape thermodynamic constraints (Schroedinger 1945). One requirement of life is that an organism must maintain a state far from thermodynamic equilibrium with the environment. Hence, all forms of life increase the entropy of the surrounding environment, while simultaneously reducing their own entropy. This idea, formulated by Prigogine and Katchalsky as "nonequilibrium" thermodynamics (Prigogine 1980), established that the exchange of energy and matter between living organisms and the surrounding environment can only occur in an open system. An equation was developed to accommodate that change,

$$\delta S = \delta_e S + \delta_i S \quad \delta_i S > 0 \tag{11.1}$$

where δS is change in total entropy, $\delta_e S$ is change in entropy resulting from exchange with the external environment, and $\delta_i S$ is the change in entropy resulting from inefficiencies internal to the system. This equation requires the system to be in a lower than maximal entropy state as long as the system can utilize energy from the environment in exchange for high entropy matter. Hence, the more complex (ordered) a living system is, the larger is the difference in entropy between living organisms and the environment.

Increased demands for both energy and order (these are independent entities) result from enhanced exchange of materials with the environment, which can be achieved either by a single organism accelerating its metabolic rate or by an increase in the population of organisms (i.e., the growth of the system). The latter principle, developed by Ladsberg (1984) and Brooks and Wiley (1988), postulates that although the entropy of a system inevitably increases over time, it will always be lower than the maximal total entropy, that is, a living system can grow without violating the second law. Using a statistical mechanical approach, Brooks and Wiley defined the maximal possible entropy (or "phase space") as a function of information and suggested that genetic information sets the upper limits of entropy.

In the evolutionary trajectory, there is a persistent increase in the organizational complexity of metazoans and photosynthetic organisms (Stanley 1973). Although the increase in complexity can be biologically attributed to competition and selection, it physically reflects an increase in the potential level of entropy, as more and more instructional information is retained. Consequently, strictly from a thermodynamic perspective, the evolution of complexity has increased the consumption of energy and low entropy materials.

HOW DOES HUMAN EVOLUTION AFFECT ENTROPY BALANCE?

The entry of *H. sapiens* onto the evolutionary stage introduced a new level of organization that simultaneously increased $\delta_e S$ and $\delta_i S$. Should humans be treated differently from the rest of evolution with respect to nonequilibrium thermodynamics, or is there simply an anthropocentric need to isolate human activities from the rest of the Universe? If the former, what feedbacks can be identified to produce sustainable human society given thermodynamic constraints?

During the course of human evolution, two major events marked the reorganization of human society and simultaneously affected planetary entropy balance. The first was the transition from a family-based hunter–gatherer existence to a tribally focused agricultural society. Examples of transitions can be found in the Natufian culture in the Levant and Jericho. The Neolithic revolution, which included domestication of plants and animals, was a turning point in the global entropy balance (Zohary and Hopf 2001), in which humans, by genetically selecting organisms, increased $\delta_i S$ at the expense of the rest of the system. This trend intensified as demands for more efficient food production for humans increased. The level of organization further increased with urbanization, which began in the early Bronze (Uruk) period.

Cities can be viewed as macro-sized dissipation mechanisms that are increasingly important in the contemporary world. They consume massive amounts of energy and low entropy matter for their maintenance, sustenance, and growth. Economy, technology, information, and social structures are an integral part of the flow of energy and matter that sustains the internal coherence of such organized superstructures. Since cities are open systems, there is no real limit to the amount of energy/matter that can be put through the system; therefore, there is no boundary on their level of complexity. Projections of supercities in the twenty-first century suggest populations within cities can grow to 25 to 50 million, requiring enormous increases in energy density. Indeed, the contemporary system demands huge amounts of energy. Global energy demand will have risen from 8.8 Gtoe (gigatons of oil equivalent) in 1990 to 11.3–17.2 Gtoe by 2020 (Birol and Argiri 1999). By the end of this century, the annual consumption is projected to reach 50 Gtoe or more.

As demand grows, there will be greater need for power plants, nuclear reactors, purification (detoxification) facilities, and depots for storage (Hoffert et al. 1998). These life-support systems are examples of yet further increases in complexity, requiring even more energy but simultaneously leading to more vulnerability to disturbance. (Witness the frequency of electrical blackouts in large sections of the United States caused by apparently trivial events.) The chance of a catastrophe en route increases in direct proportion to energy and material demands. At some point in this unfolding thermodynamic drama, the planet must plunge into a high-energy, low-entropy "trap," from which it will be increasingly difficult to escape. Clearly it is preferable to avoid the trap than to develop escape strategies *post facto*. One potential avoidance strategy employs altruism.

EVOLUTION AND ALTRUISM

Selection operates on individuals as manifested by phenotypic expression. Fitness, defined as the production of viable progeny, operates at the level of individuals and, barring a catastrophic mass extinction, determines the evolutionary trajectory of a species. As such, *intraspecific altruism*, which we define as a *reduction in reproductive output* by one individual in order to enhance the reproductive success of another, has no net effect on population growth but does affect phenotypic expression. Although there are many examples of altruistic behavior in vertebrates, it is a relatively rare behavioral characteristic outside of humans and other primates. In humans, however, altruism flourishes and is promoted culturally as an outgrowth of ethical knowledge. Altruism is not manifested by all individuals and does not appear to be genetically inherited. Therefore, we suggest that there is a third level of human knowledge, operating at the level of the individual, which we will simply call *individual knowledge*.

We propose that individual knowledge is obtained experientially as part of the developmental process, through parents, societal interactions (e.g., early childhood play, storytelling, and interactions with elders), and through cultural (tribal) rituals (e.g., religion, political structure). Because altruism is learned, it can be taught — and hence can rapidly pervade human society — but it can be lost just as rapidly. In the evolution of modern, (especially) Western, societies, the confluence of uneven accumulation of wealth and ethical knowledge gave rise to increased pressure for altruism. Altruistic behavior, manifested, for example, in the redistribution of wealth or its application to large segments of society (e.g., the creation or endowment of a university, library, or hospital) can have a positive feedback. Ultimately, however, the accumulation of wealth, coupled with altruism and distributed knowledge, perpetuated a group of individuals who specialize in science and technology. These latter individuals have provided human societies with the tools and abilities to plunder resources more rapidly and are often looked to by other members of those societies for solutions to problems that innately require individual altruistic behavior. Indeed, scientists and technicians can manipulate genetic information and, in so doing, rapidly alter the phase space of the planet.

NONLINEAR OUTCOMES FROM ALTRUISTIC BEHAVIOR

Altruistic behavior can temporarily increase the evolutionary fitness of humans, but it can also have unintended negative impacts on the environment. We use, as an example, U.S. government policy at the end of World War II. To help returning veterans readjust to civilian life (and to help the economy), laws were passed that were ostensibly altruistic (by redistributing wealth), promoting the purchase of single-family houses outside of urban centers. Suburbia was born. The rapid expansion of single-family houses adjacent to cities (a phenomenon almost unique to the U.S.A.) fostered increased resource plunder. The development and expansion of suburbia destroyed farms and open spaces, replacing these not only with houses and schools and shopping centers, but with multilane highways, degraded lands, reduced habitat for other species, and gross overutilization of groundwater. This is an illusory reduction in entropy.

In suburbia, distributed transportation is virtually impossible. Americans became enamored with cars. Within a single generation, two energy-consuming (i.e., high energy, low entropy) pathways — a single-family house and one or more automobiles — became the norm for millions of Americans and remains so to this day. The net result is that government policy (or lack thereof) coupled with ignorance and arrogance (a lack of ethical knowledge) and only small numbers of altruistic consumers have produced the largest fossil-fuel demand ever seen on this planet. These types of nonlinearities in development can have profound negative effects on resource use and habitat. Songbirds, butterflies, and wildflower populations are decimated throughout much of the U.S. — victims of herbicides and insecticides designed to maintain perfect, "weed-free" lawns. Chlorine evasion to the atmosphere increases dramatically in the summer months as individual houses have individual swimming pools which consume annually millions of kilograms of chlorine.

The nonlinearities also affect societal structure. During World War II, the U.S. army segregated African-American soldiers from white soldiers. There

were relatively few African-American draftees — most African-American males worked in factories in support of the war effort. These, nonmilitary personnel were not eligible for the housing subsidies and hence remained in the central cities. Those African-American veterans who tried to find a house in suburbia were often subject to discrimination. The government tax policies effectively (and inadvertently) promoted "white flight" and increased the racial segregation of America — a problem that remains and profoundly influences social structure and the distribution of wealth in the country to this day.

There are other, more dramatic examples, including the deforestation of Amazonia for short-term crop production, cattle ranches, and timber harvesting. In this case, government negligence and corruption rather than altruism are primary drivers. Similarly, strip mining in Africa, Australia, and China has led to massive alterations in surface topography which, in turn, has altered habitats for animals forever. Redistribution of water, for the production of energy and irrigation of crops, inevitably alters habitat as well. These and other activities, including expansion of grazing land and elimination of top predators, have massively altered the population structure and controls on most herbivorous mammals on the planet. Naiveté has played a role as well. The deliberate importation of mongooses to Hawaii and other islands, ostensibly to eat rats, another introduced species, led to a massive extinction of birds. Mongooses love bird eggs - they do not eat rats. Biological homogenization and direct exploitation (for food) has contributed to a rapid decrease in many species in a short time. Birds are very scarce in modern China - most have been eaten by humans. Codfish are almost extinct in the Northwest Atlantic - they have been efficiently harvested through the distributed technological knowledge of a more advanced species that seeks wealth (Jackson et al. 2001).

Social fixes to these complex problems are often hard to find. For example, a tax code could easily be written that would foster the return of people from suburbs to cities; however, there is no political motivation to do so. As long as energy and land are relatively affordable, suburban saturation is likely to persist and that is hardly a path to sustainability. Extinction is forever — and although habitats can be restored, it does not mean that species will return. Is the sentimentalization of nature an important component of *ethical knowledge?*

THE ROLE OF SCIENCE

Over the past thirty years or so, scientists have increasingly documented the effects of humans in plundering Earth's resources. The documentation has had a relatively modest effect on societal responses. Sustainable development requires the mass expansion of individual altruistic behavior, a process that itself requires education and a reevaluation of how human economic structures can be used to preserve and conserve natural resources for future generations of humans. Education in developed countries can markedly alter patterns of resource use, but this must be coupled with intelligent investment of wealth in technologies that are inherently sustaining. For example, the photocatalyzed extraction of hydrogen from water would provide a potentially limitless, clean energy source, yet in the U.S. the investment in this process is less than \$10 million per annum. A single breakthrough in catalysis could change the world forever. Similarly, the production of long-term human contraceptives, the development of N₂-fixing crops, or the replacement of relatively rare metals (such as titanium) in machines with easily produced alternative materials derived from renewable resources can alter the course of human impact on Earth.

Science and technology, however, are not the only solutions — human ingenuity must be coupled to human behavior. The concept that humans are partners in ecosystems is not new, but it does not pervade the human psyche, except in isolated, nomadic tribes, where there is a clearer, intuitive appreciation for habitat and a respect for it. We must leave the "documentation" stage of scientific enquiry and enter a social/technological stage, where realistic outcomes (both positive and negative) can be envisioned and integrated solutions explored. Nonlinearities in policy that can lead to dramatic changes in human behavior should be identified. Science does not simply serve as a knowledge base — it must also serve as a conscience of society — reminding wealth "creators" that sustainable resource management is the only viable option for future generations.

ACKNOWLEDGMENTS

We thank NSF and NASA for supporting our research as well as Andi Andreae, Andrew Irwin, Simon Levin, Peter Smouse, and Tamar Zohary for constructive comments on the manuscript.

REFERENCES

Becker, E. 1997. The Denial of Death. New York: Simon and Schuster.

- Berman-Frank, I., P. Lundgren, Y.-B. Chen et al. 2001. Segregation of nitrogen fixation and oxygenic photosynthesis in the marine cyanobacterium *Trichodesmium. Science* 294:1534–1537.
- Berner, R.A., S.T. Petsch, J.A. Lake et al. 2000. Isotope fractionation and atmospheric oxygen: Implications for Phanerozoic O₂ evolution. *Science* 287:1630–1633.
- Birol, F., and M. Argiri. 1999. World energy prospects to 2020. Energy 24:905-918.
- Blankenship, R.E. 2001. Molecular evidence for the evolution of photosynthesis. *Trends in Plant Sci.* 6:4–6.
- Brooks, D.R., and E.O. Wiley. 1988. Evolution as Entropy: Toward a Unified Theory of Biology. Chicago: Univ. of Chicago Press.
- Carroll, S.B. 2003. Genetics and the making of Homo sapiens. Nature 422:849-857.
- Conley, D.J. 2002. Terrestrial ecosystems and the global biogeochemical silica cycle. *Global Biogeochem. Cycles* **16(4)**1121.
- Delwiche, C.F. 1999. Tracing the thread of plastid diversity through the tapestry of life. *Am. Naturalist* **154**:S164–S177.
- Epstein, E. 1994. The anomaly of silicon in plant biology. *Proc. Natl. Acad. Sci. USA* **91**: 11–17.

- Falkowski, P.G. 1997. Evolution of the nitrogen cycle and its influence on the biological sequestration of CO₂ in the ocean. *Nature* **387**:272–275.
- Falkowski, P.G. 2001. Biogeochemical Cycles. In: Encyclopedia of Biodiversity, vol. 1, ed. S. Levin et al., pp. 437–453. San Diego: Academic.
- Falkowski, P.G. 2002. On the evolution of the carbon cycle. In: Phytoplankton Productivity: Carbon Assimilation in Marine and Freshwater Ecosystems, ed. P. le B. Williams, D. Thomas, and C. Renyolds, pp. 318–349. Oxford: Blackwell.
- Falkowski, P., M. Katz, B. van Schootenbrugge, O. Schofield, and A.H. Knoll. 2003. Why is the land green and the ocean red? In: Coccolithophores: From Molecular Processes to Global Impact, ed. J. Young and H.R. Thierstein, pp. 429–453. Berlin: Springer.
- Falkowski, P., R.J. Scholes, E. Boyle et al. 2000. The global carbon cycle: A test of our knowledge of Earth as a system. *Science* 290:291–296.
- Hayes, J.M., H. Strauss, and A.J. Kaufman. 1999. The abundance of ¹³C in marine organic matter and isotopic fractionation in the global biogeochemical cycle of carbon during the past 800 Ma. *Chem. Geol.* 161:103–125.
- Hoffert, M.I., K. Caldeira, A. Jain et al. 1998. Energy implications of future stabilization of atmospheric CO₂ content. *Nature* 395:881–884.
- Jackson, J.B.C., M.X. Kirby, W.H. Berger et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–637.
- Kasting, J.F., O.B. Toon, and J.B. Pollack. 1988. How climate evolved on the terrestrial planets. *Sci. Am.* 258:90–97.
- Knoll, A.H. 2003. Life on a Young Planet. Princeton: Princeton Univ. Press.
- Ladsberg, P.T. 1984. Can entropy and "order" increase together? *Physics Lett.* 78A:219–220.
- Lenton, T., and A. Watson. 2000. Redfield revisited, 2: What regulates the oxygen content of the atmosphere? *Global Biogeochem. Cycles* 14:249–268.
- Lieberman, P. 2000. Human Language and Our Reptilian Brain: The Subcortical Bases of Speech, Syntax, and Thought. Cambridge MA: Harvard Univ. Press.
- Lovelock, J.E. 1979. Gaia: A New Look at Life on Earth. Oxford: Oxford Univ. Press.
- Nealson, K.H., and P.G. Conrad. 1999. Life: Past, present and future. *Phil. Trans. R. Soc. Lond. B* 354:1923–1939.
- Prasil, O., N. Adir, and I. Ohad. 1992. Dynamics of photosystem II: Mechanism of photoinhibition and recovery processes. In: The Photosystems: Structure, Function, and Molecular Biology, ed. J.R. Barber, pp. 295–348. New York: Elsevier.

Prigogine, I. 1980. From Being to Becoming. San Francisco: W.H. Freeman,

- Rothman, D. 2001. Global biodiversity and the ancient carbon cycle. *Proc. Natl. Acad. Sci. USA* 98:4305–4310.
- Sage, R.F. 1995. Was low atmospheric CO₂ during the Pleistocene a limiting factor for the origin of agriculture? *Global Change Biol.* 1:93–106.
- Schroedinger, E. 1945. What Is Life? Cambridge: Cambridge Univ. Press.
- Stanley, S.M. 1973. An explanation for Cope's rule. Evolution 27:1–26.
- Sykes, B. 2001. The Seven Daughters of Eve. New York: W.W. Norton.
- van Valen, L. 1973. A new evolutionary law. Evol. Theory 1:1–30.
- Vitousek, P., H. Mooney, J. Lubchenco, and J. Melillo. 1997. Human domination of Earth's ecosystems. *Science* **277**:494–499.
- Zohary, D., and M. Hopf. 2001. Domestication of Plants in the Old World: The Origin and Spread of Cultivated Plants in West Asia, Europe, and the Nile Valley. Oxford: Oxford Univ. Press.