Chapter 1

ECONOMY AND EVOLUTION: A ROAD MAP

We live in a changing world, in an economic context of competition and resources to which we and our forebears have both adapted and contributed. It is impossible to separate us and other life forms from that context, for the context determines our character and we determine its character. If we wish to understand the past and the future, we must discover how the link between life and its context changed in history, to what extent economic change is predictable, and how the principles governing competition-driven demand and resource-driven supply intersect to yield laws of history.

At its core, this book is an economic analysis of history. In it, I argue that economic principles applicable to humans are the same as those that govern all other forms of life. The patterns of history that emerge from these principles are therefore universal, even if the details of timing and actors vary according to time and place.

It is easy to get lost in the fascinating phenomenology of economic history—in the particulars of places, participants, events, behavior, relationships, patterns of descent, and the like—and to lose sight of the structure of the arguments and of the principles on which these arguments rest. I therefore begin with an outline of the main points, with a road map to the sometimes tortuous path of the narrative that follows as it takes us through past and present ecosystems around the world.

Although we usually think of the word *economy* in such human terms as trade, profits, markets, and finance, it applies just as aptly to the systems of which living things other than humans are constituents and architects. In chapter 2 I lay out what I hold to be the fundamental characteristics and principles of economies. An economy is a collective whole, a system of metabolizing, interacting, smaller units or entities that are themselves economies. The constituent units adapt to, and bring about changes in, their environment as they compete locally for energy and material resources. Economies are built on living things, which complete cycles of work by coupling chemical transformations that alternately use and release energy in the context of an architecturally and organizationally constrained physical structure. Economies thus have knowable properties not possessed by any one of their individual members. The work of life—growth, replication, and activity—creates meaning and information and ultimately leads to a history in which self-interested parties who cooperate to fashion larger wholes give rise to and replace each other. Evolution—descent with modification—is thus an expected and universal historical process in economic systems. It occurs because economic units compete locally for resources, and because only those entities that acquire and retain the necessities of life in the face of such competition and of uncertainty persist. Cooperation among economic players reduces rivalry at one level, but creates more potent competitors on a larger scale. Trade and cooperation (or mutual exploitation) thus lead through self-organization, or co-construction, to regulation of resource supply and consumption, and to complex interdependencies that emerge as the common good for the larger economy and for many of its constituents, especially for those that wield disproportionate power.

Energy or its equivalent is what economic systems or their members exchange, but power—the amount of energy produced, consumed, or retained per unit time—is the best measure of absolute performance of living things. To the evolutionary biologist, absolute performance is usually expressed as fitness, the number of offspring in the next generation; to the economist, it usually translates into profits. Although we often think of words like economy or economical in terms of efficiency—the amount of energy gained per amount of energy invested—it is absolute power rather than efficiency that matters in the economies of nature and human affairs. Selection (or nonrandom elimination) operates whenever entities differ in performance-related characteristics that are heritable in some way. The universe works, and life works and persists, because we co-construct our universe through the combined processes of modification and selection. Adaptation, the process resulting in a better fit between entities and their environment, is universal among living things, which create and improve hypotheses about their surroundings much as scientists propose and test hypotheses explaining observations and regularities in the world.

For a variety of reasons, adapted entities are inevitably imperfect, and thus in principle are capable of improvement. Some challenging circumstances are simply too infrequent for an entity of limited lifespan to predict; others call for adaptive solutions that are in conflict with the demands imposed by different challenges, so that an imperfect compromise reflecting functional tradeoffs becomes the most likely option. Moreover, information about the environment is never either complete or accurate, a situation often exacerbated by the actions of competitors. Economic units and the coalitions they form create hypotheses about their environment that are as good as they have to be relative to the hypotheses of their competitors. Where competition is intense—where the consequences of losing are dire and the benefits of winning are great—the standards of performance and the predictiveness of adaptive hypotheses must be high. Where the stakes are lower, or where there is more tolerance of error, trade-offs are less constraining and persistence, or economic success, is achievable with lower levels of performance and with more generalized hypotheses. In other words, living things do only as well as they have to rather than optimize, pretty much as students do in classes.

One of the most pervasive and far-reaching realities in economic systems is inequality, the tendency for one party involved in an interaction over resources to gain more, or lose less, than its rival. Dominants exercise disproportionate influence and accumulate disproportionate power and wealth. Through top-down control, they affect not only the characteristics and distribution of other members of the economy, but they define the structure and workings of the economy as a whole. Inequality and dominance occur at all scales of economic life, from the cell to the biota, from the household and firm to international relations. They are expressed at all scales of time, from the life cycles of cells to the long-term replacements observed among empires and the great evolutionary branches of life. Inequality does not mean that the winners succeed while the losers fail. Winners can be, and often are, replaced, and although the losers are often restricted to the economic margins where resources are less plentiful and less reliable, the entities with subordinate economic positions may enjoy long periods of stability. In fact, the refuges in which they find themselves are often created by the winners, and as long as such refuges exist, the losing parties and their adapted descendants not only survive, but are often at the forefront of economic expansion into underexploited domains of the biosphere.

The fundamental processes operating in economic systems—competition, cooperation, selection, adaptation, and the feedback between living things and their environment—apply to all such systems, from those as small as a cell to human societies and to the biosphere as a whole. They work regardless of the particulars of how performance-related characteristics are introduced, inherited, modified, or eliminated. Importantly, they have characterized life since its beginning some 3.5 billion years ago, and they have been responsible for unbroken evolutionary lines of descent chronicling continuous success in the face of startling long-term change, devastating disruptions, and ever-present struggles over resources.

It is all well and good to characterize the domain of nonhuman life as a hierarchy of economies ruled by competition, cooperation, adaptation, and inequality, but does this perspective have anything useful to say about human economic life and civilization? There is a long history of claiming for humanity all sorts of unique attributes—language, intentionality, cultural transmission of knowledge, anticipation of future conditions, moral codes, the ability to use previously unexploited sources of energy, and more—to say nothing of the unique institutions that dot the landscape of civilization: schools, corporations, governments, stock markets, farms, factories, shops, prisons, churches, banks, amusement parks, and so on.

I argue in chapter 3, however, that the human species and the human economy do not differ fundamentally from units encountered in the rest of the biosphere. Humans are without question the most powerful economic entity that has yet evolved on Earth; we accomplish things on spatial scales vastly larger than any other species, and our unparalleled power enables us to do everything much faster by orders of magnitude than is possible in any other economy that arose on Earth. We anticipate and predict; we modify environments globally, and exercise control over every ecosystem on this planet. Yet, in spite of all these unique qualities and institutions, our species and the economic and social system we have created follow all the same fundamental rules that govern other life forms and their economic structures. Like other living things, we too are ruled by conflicts of interest, cooperative behavior, adaptation, unequal outcomes of trade, the disproportionate influence of the rich and powerful, and the vagaries of resource supply that dictate when and where opportunities are created and constraints are imposed. None of our attributes has thus far enabled humans to violate the principles that apply to all other life forms. Life and its history therefore have much to say about ourselves, including our future. Moreover, all of our unique characteristics are derived from precursors observable in nonhuman life forms. Cultural (or at any rate nongenetic) transmission of performance-related information, machinery, and behavior has existed since life's origin; and our ability to modify and to anticipate has obvious, if less spectacular, precedents in the adaptations and the mechanisms of adaptation in other organisms.

Having laid out the rules common to all economies, I turn to the two activities—consumption and production—that together describe what living things do. Predation—the consumption of living things by other living things—invests the abstract ideas of chapters 2 and 3 with real life-and-death significance in chapter 4. Here we meet potential victims who face daily confrontations with, and risks from, enemies. Their defenses range from the passive—cryptic coloration, toxicity, and heavy armor—to more active means such as fleeing and aggression. Those victims without effective defenses are restricted by their enemies to refuges, safe sites where predators are themselves physically constrained. Thus, we find life forms on the bodies of well-defended large organisms, or deeply buried in soil, or floating in the plankton, or cowering in the inhospitable border between sea and land, or populating temporary habitats.

We also meet the predators themselves, animals among which competition for food is intense and whose feeding methods and abilities are dictated largely by performance during encounters with rivals. Predator and prey respond to one another directly behaviorally and even architecturally, but in an evolutionary sense it is the predators in particular, and enemies in general, who hold the upper hand. In all ecosystems, at least some predators exceed all potential prey in energy-demanding performance. They have more acute senses, move or maneuver more rapidly, and exert greater forces than do their victims. It is only in passive performance—toxicity, armor, and large body size—that potential victims exceed their enemies in performance. Given that passivity is usually linked to inactivity, predators exercise far more control over the characteristics of living things—their behavior, form, and distribution—than do victims. Powerful consumers, with high per capita and collective rates of consumption, drive economic systems and impart structure and direction to them. They impose pervasive top-down evolutionary and economic control, because adaptation to enemies characterizes all members of all economies. In short, adaptive evolution is largely a process of escalation in which potential victims adapt to enemies, which in turn adapt or accommodate to their enemies.

Consumers may evolutionarily control the characteristics and distribution of life, but they cannot exist without producers. In chapter 5, I explore how primary producers—microbes, plants, and phytoplankton, which make organic matter from inorganic components—compete for energy and raw materials. Resources often appear to be globally superabundant—think of energy from the sun, nitrogen in the atmosphere, and silicon in the sand, for example—but they limit productivity because competition for them is local, and because access to them is constrained by the technology of extraction, storage, conversion, and distribution. Resources and the creatures that convert them to biomass exercise pervasive, diffuse, bottom-up controls over economic systems and their constituents. All living things are in some sense producers, and all provide potential resources to other life forms. A surplus of production—that is, the amount produced beyond the requirements of the producers themselves—determines how much consumption an economy can support sustainably. It, in turn, depends on the ability of victims to thwart consumption, often through passive means. Resource supply and anti-consumer adaptation thus set limits to the amount and nature of consumption through a series of complex positive and negative evolutionary and economic feedbacks. Abundance and access provide evolutionary and economic opportunity for adaptation and growth; scarcity and lack of access impose constraint.

Forms of consumption that stimulate production will in general be favored over those that interfere with it. By consuming living plant matter, for example, herbivores circumvent some decomposers and therefore recycle nutrients faster than if nutrient transfer from plants were exclusively in the hands of organisms that consume dead tissues. Organisms tend to regulate and often improve the supply of resources so that the supply becomes reliable and high enough to support populations of consumers. For example, predators that eat snails without destroying the shells of their victims create a reasonably steady supply of shells for hermit crabs, which in the absence of such consumers would be at the mercy of rare storms or other unpredictable events to make empty shells available. Functional links between producers and consumers thus create a more productive, more opportunity-rich economy in which conditions for the common good of both dominant and subordinate members emerge.

Energy is the currency of economic exchange and value, but power—the rate at which energy and raw materials are used—is the measure of economic performance. More power means more control. In part, power is derived from the environment. The ability to respond adaptively, to improve hypotheses about the environment, and to capitalize on opportunity depends on how rapidly and how reliably the environment delivers resources, but it also depends on the technology that economic entities possess. In chapter 6, I explore the architectural and organizational qualities that bestow power, wealth, and adaptability on living things. Powerful entities are large, metabolize rapidly, have a wide individual or collective reach, and possess a flexible, hierarchical organization characterized by semiautonomous interacting parts subject to diffuse central control. Cooperation, division of labor, effective communication among parts and among individuals, and an ability to respond rapidly and flexibly under a very wide variety of circumstances, including rare ones, characterize all economically powerful entities. Power provides access to resources, and this power stimulates production and all other processes that confer greater power in the first place. It is therefore a great amplifier of economic life, an attribute which depends on, and in turn promotes, intense high-stakes competition.

The technological and organizational qualities that bestow economic and physical power will increase only if the benefits of greater power exceed the high costs of investment in power-enhancing innovations. Such large outlays become feasible only when resources are abundant, accessible, and predictable in economies of large effective size in which competition is intense. It is only under such circumstances that entities are able to modify patterns of allocation and where large imperfections of innovations are able to survive long enough without lethal consequences for selection to improve them. Conditions favoring increases in the sizes and numbers of individuals and groups thus provide opportunities for improvement and growth by reducing the cost of imperfection and by relaxing the constraints of trade-offs that under economic stagnation or decline enforce an adaptive status quo.

Four interrelated factors and processes in the environment—temperature, the effective size of economies, heat-powered eruptions and tectonic movements of Earth's crust, and life's metabolism—together determine the supply of resources and therefore the distribution of opportunity and constraint in space and time on our planet. I consider this environmental component in chapter 7.

Temperature—the average kinetic energy of molecules moving in a fluid or gas—affects almost every chemical reaction and material property on which life depends. A rise in temperature from the freezing point of water to somewhere between 35 and 40°C, above which the molecules of life begin to suffer heat-related loss of function, enables organisms whose body temperatures approximately match those of the surroundings to accomplish the work of life faster and often more cheaply, and thus to draw and deliver more power. Animals can move and feed faster, growth rates are potentially higher, and microbes and plants extract limiting mineral nutrients more quickly as they chemically break down rock and soil. At higher temperatures, such viscosity-related activities as filter-feeding and swimming in water become cheaper because the surrounding medium becomes less sticky and therefore less resistant to flow. Perhaps most importantly, they make available a much wider range of adaptive possibilities. In the cold, everything is slow, and there is little difference between the fastest and slowest members of a community. Under warm conditions, adaptive solutions emphasizing rapid movement and growth coexist alongside solutions featuring inactivity or slow accumulation. Higher temperatures therefore permit more extreme patterns of energy allocation and functional specialization in more directions, and allow the realization of adaptations that are unachievable in cold-bodied creatures.

Although maintenance costs tend to rise with increasing temperature, the power-related benefits of operating under warm conditions are greater as long as sufficient resources exist to maintain the fast-running engine of life. For this reason, warm-blooded animals—birds, mammals, some insects, and even some fish—capable of producing capable internal body heat for extended periods hold prominent economic positions of power in most of the world's ecosystems, despite their great inefficiency. Moreover, by achieving a degree of thermal independence, they can operate effectively as active competitors under a very wide range of circumstances.

Small economies set severe upper limits to the per capita and collective power of their members. For large-bodied or rapidly metabolizing creatures, small economies imply small populations, which are more vulnerable to disruptions than large ones. The effective size of an economy—the area or volume of "suitable" habitat—depends both on the physical structure of the environment and on the locomotor and physiological responses of living things to it. For wide-ranging individuals or species, the economy is effectively larger than for a sedentary one. All else being equal, the largest land masses and water bodies tend to be the most permissive locales for entities of high performance, whereas isolated small islands support more slowly metabolizing types.

Materials cycle into and out of the biosphere on time scales dictated by both geological and metabolic processes. Volcanoes and undersea vents carry nutrients, including the greenhouse gas carbon dioxide, from the mantle and lower crust to the surface. Collisions between continental blocks, and sites where one block rides over and subducts another, are associated with mountain building. Wind, ice, and water physically break down the new surface rock and transport the eroded debris into rivers, lowlands, and the coastal zones of oceans, where organisms further break the fragments down to release soluble mineral nutrients. The formation of new crust beneath the seafloor raises sea level and indirectly creates large areas of high productivity in moist lowlands and shallow coastal seas. The release of carbon dioxide attending the formation of new crust warms the world and thus stimulates production and consumption still further. High temperatures and high production conspire to cause not only more consumption, but also the burial of a larger amount of organic matter, a process that in turn releases more free oxygen to the atmosphere by preventing oxidation of some of the biomass that is buried. Positive feedbacks among producers, consumers, and the geologically and celestially controlled environment of Earth magnify the stimulatory effects of external inputs and create productive ecosystems in which selection due to competitors and other enemies is intense.

The conditions of life—risks, rewards, opportunities, and constraints—vary greatly from place to place on many spatial scales, over millimeters for microbes to thousands of kilometers for ecosystems. In chapter 8 I examine this variation on the scale of geography. Although the physical structure of Earth's surface—the distribution of oceans, land masses, rivers, sediments, rainfall, and temperature, among other features and factors—in part determines where particular types of organisms and ecosystems exist, living things themselves profoundly influence the geography of life. Competition and specialization create and dissolve barriers that define the limits of distribution of species and the economies to which they belong. The geography of life therefore reflects a complex interplay between Earth's intrinsic heterogeneity and the superimposed, competition-related heterogeneity imposed by life itself, much as the geography of humanity reflects cultural and political patterns on the physical landscape.

Regions and ecosystems in which productivity is high, competition is intense, and adaptation is least constrained by energetic and material limitations, occur at low to middle latitudes—the tropics and subtropics, in other words—in moist lowlands and the shallow waters of oceans near large, topographically complex land masses. These environments and the species living in them economically and evolutionarily subsidize less productive parts of the biosphere with raw nutrients, food organisms, and evolutionary lineages; they thus act as donor regions and dominant species on a geographic scale. Species invade from the tropics to the temperate zone, not in the opposite direction. There are far more invasions from the sea to freshwater than in the opposite direction, except among vertebrates capable of functioning actively under a wide range of circumstances. Initially, the sea economically and evolutionarily subsidized the dry land, but beginning some 300 million years ago, after land plants had achieved the stature of forest trees, more lineages invaded from land to sea than from sea to land. Large regions—land masses such as Eurasia, Africa, and to a lesser extent North America—and marine regions such as the Indo-West Pacific tropics produced many competitively superior entities that have spread far outside their original ranges into smaller, less productive regions.

In line with this geographic pattern, the origin of hominids and of modern humanity in competitively rigorous Africa, and the rise of early agriculture in the extensive fertile lands of the Fertile Crescent, south Asia, and China is not surprising. Productivity, power, and innovation continue to characterize large, opportunity-rich economies and societies in the human domain.

There is also a historical dimension to the pattern of subsidy among the world's major biological regions. Areas whose biotas have suffered less extinction of species tend to support competitively more sophisticated species, which have spread to biota that have suffered significantly more disruption. The removal of well-adapted incumbents thus allows plants and animals to become established even if these species are not initially well adapted to the conditions of life in the newly available habitats. As we humans increasingly eliminate incumbent species while transporting many others around the world, opportunities for successful establishment are expanding greatly, sometimes with disastrous consequences.

These relationships underscore the central importance of disruption. I treat this universal phenomenon and its consequences in chapter 9. Because economic entities tend to be well adapted to their surroundings, any change in those surroundings is apt to be harmful. All economic systems and their members are vulnerable to disruption, that is, to instability imposed either from the outside or from within the system. Storms topple trees, fires devastate forests, hunters extinguish populations of large animals, droughts bring societies to their knees, and cataclysmic geological upheavals—massive volcanic eruptions, exhalations of methane gas from great reserves beneath the ocean floor, and especially impacts of asteroids and comets—buffet and sometimes cause the collapse of economies large and small.

I argue that bottom-up disruptions, those interfering with the delivery and regulation of resources and the means of production, are far more destructive than are the major instabilities caused by the elimination of only top consumers. Interruptions in primary production not only remove the necessary resources for those herbivores, suspension-feeders, and predators that depend directly on primary producers for food, but also destroy the three-dimensional structure in which individuals find refuge from consumers. If the machinery of production remains largely intact, and chiefly the top consumers—large herbivores, carnivores, and suspension-feeders—are removed, as has been the case up to this point in the human-dominated biosphere, the dramatic changes in ecosystem composition are not accompanied by widespread collateral extinctions. For example, the human-caused disappearances of most of the large mammals in North and South America and Australia following the arrival of humans on those continents led to great irreversible alterations in the vegetation, but most other species were able to persist, albeit in a markedly different biological environment. The same applies to the oceans, from which humans have eliminated or drastically reduced populations of most larger predators and herbivores.

All of the mass extinctions, and probably most of the so-called minor episodes that punctuate the history of life, are associated with the disappearance of much of the phytoplankton in the ocean and the land-plant producers on the continents. Similarly, the demise of ancient human civilizations is often linked to droughts and other circumstances that reduce the primary production on which human society ultimately depends. Interference with sunlight through the formation of giant dust clouds following the impact of celestial bodies seems to be the most plausible mechanism for precipitating global collapses in primary production during the most severe economic disruptions.

But there is also a bright side to disruption. Short-term disturbances enable fast-growing species with high metabolic rates and with inert life stages capable of withstanding adverse conditions to capitalize on briefly favorable circumstances, and it is these opportunists that are in the best position to spawn highly competitive dominants in postcrisis ecosystems from which well-adapted incumbents have been eliminated. The rare, extinction-causing disturbances thus give opportunities to new invaders for which there is a premium on rapid establishment and rapid exploitation. High-powered survivors therefore have a critical advantage during the recovery from crises.

This stimulatory role of disturbance in spreading rapidly metabolizing opportunists and their competitively superior descendants exemplifies the central thesis of this book, laid out in chapter 10: inequality, as manifested by the power and wealth of economic players with disproportionate control over others, imparts an overall directionality to the historical development of economic systems, including our own. Successive dominants at every scale of organization become more powerful, more productive, and internally more diversified, and they increase both their reach of control and their independence from their environment. Life itself increases opportunities for growth and adaptation while reducing constraints. Disturbances interrupt and occasionally reverse these trends, but in the long run they enhance rather than thwart these trends. Events that trigger or disrupt overall trends determine the time course of historical processes. We cannot know their timing in advance, nor can we predict the precise nature of the participants and the interactions in which they are engaged; but these accidents and contingencies of history, important as they are, do not undermine or invalidate the claim that economic history is inherently directional.

In the history of life, directionality and contingency can be seen over the time span of billions of years. We see plants and animals partially eclipse bacterial-grade microbes, warm-blooded vertebrates succeed cold-blooded ones as the dominant consumers of their age, fast-growing flowering plants push slower-growing ferns and conifers out of low latitudes and rich soils, and heavily armored or exceptionally fast molluscs increasingly replace older groups with less specialized shell defenses and slower life-styles. The parallel history of humanity plays out on the much shorter time scale of decades to thousands of years, but the patterns as chronicled by the rise and fall of empires, the invention of new means of extracting energy, and the increase in the magnitude and reach of trade mirror those seen on the long time scale of the history of the biosphere as a whole.

What do the conclusions about power and history portend for our future? I consider this question in the final chapter. On the one hand, nature has given us innumerable past and present examples of economic structures that endure and adapt sustainably in the face of predictable and unpredictable change. On the other hand, all economic activity brings about change, and it does so in broadly predictable ways—toward greater productivity, diversity, and power—all the while creating higher-order emergent entities. Human history has mainly fallen in line with these long-term trends, but our unprecedented power has enabled us to throw the economic system out of a state of orderly change and harmony into one of instability and chaos. During the past three centuries, there have been vast and rapid increases in human population size, per capita and collective energy use, individual lifespan, trade, material wealth, the rate of invention, the directed gathering of scientifically acquired knowledge, and opportunity. We engage in arms races of unprecedented magnitude, and we are changing the economic structure of the biosphere so rapidly that our and others' ability to adapt is increasingly in doubt. We have come to depend not just on growth, an attribute that has always enabled adaptation in economic systems, but on very rapid growth.

In the very long term, such rapid growth is unsustainable for those of us who remain on and depend on the Earth. Sooner or later, despite all the economic substitution of resources and all the efficiency we can still build into our economic system, we will reach a limit. When we reach it, this limit will impose a regime of rigid conservatism in which adaptability and opportunity, including the scientific acquisition of knowledge, the solution of problems, and funding for the finer things of life will be severely curtailed. This is a type of stability that few would find desirable.

The preservation of economic growth well below the threshold between order and chaos would seem most ideal, not least because this is the regime that has endured and enriched the biosphere from the very beginning. It stimulates individual opportunity, and permits investment in science, the only method of discovery and problem-solving that precisely parallels adaptive evolution. Based on 3.5 billion years of history, I find it inconceivable that humanity and any of its most powerful individuals or institutions will voluntarily choose to cede power and to forego economic expansion. Instead, we must endeavor to create a system in which no part of humanity, nor the human species as a whole, gains so much monopolistic, centralized power that regulation and competition disappear. Given that all sustainable natural systems, from developing embryos to physiologically functioning bodies, are characterized by diffuse regional regulation and local control, it would be wise for us to model our own institutions, from governments to corporations, on such adapted economies. We cannot eliminate power or inequality, but we can regulate and use them to create a common good at the largest possible scale—that of the Earth as a whole—by intentionally designing flexible, responsive, accountable structures in which all elements participate and in which opportunity and adaptation are allowed to lead to slow growth. We are unlikely to break the laws of economies or to alter the course of economic history. We should therefore use them to our best collective advantage by learning how nature provides opportunity, adaptation, and constraint.