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A Historical Conspiracy: Competition, Opportunity, and the Emergence of Direction in History

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I describe historical patterns that I believe would emerge in any system characterized by living things competing for locally scarce resources. I then consider the search for patterns and their explanation in the context of an intellectual climate dominated by anti-adaptationist rhetoric and doubts about the validity of scientific approaches to history. Notwithstanding this hostile environment, I present a summary of the economic principles that in my view not only account for historical patterns but also serve to predict future trends and postdict past ones not yet known. A positive feedback between consumers and resources – a historical conspiracy of sorts – implies the existence of inherent directions in the history of living things, including humans.

Introduction

Alfred Fischer's baritone filled the room when he lectured. I sat transfixed as he painted mental pictures of continents splitting and colliding, the world coming alive with animals at the dawn of the Cambrian period, and relatives of ancient squid swimming about with their long, clumsy, gas-filled shells in an Ordovician sea. He described massive bouts of extinction, subsiding coastal basins in California filling with sediments and leaving a record of stability and change as chronicled by tiny planktonic foraminifers, and the structure of ancient Paleozoic reefs. Here was history writ large, a grand story of life back to its beginnings as revealed by the geological record. Strange animals and plants from far-away places and remote times witnessed events of unimaginable scale. The narratives Fischer so evocatively brought to life were every bit as gripping as the more familiar accounts of human history.

But unlike the written record of human events as interpreted by traditional historians, the chronology that Fischer sought to reconstruct was founded on science. Meticulous observations on ancient rocks and fossils were supplemented with insights from experimental and comparative biology to establish not only a temporal framework of life's evolution, but also with hypotheses of the conditions under which ancient forms of life existed. The love of seashells I had had since childhood was rapidly expanding into a love of historical science during my time at Princeton, where Fischer and others

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helped shape my scientific orientation. I wanted not only to describe the phenomenology of present and past life, but also to look for and to explain patterns. Without ignoring the welter of fascinating descriptive details of living and ancient nature, I sought basic principles; I wanted to become a Bigstoryan.

My approach would be comparative. Relying on experimental work in living systems, I would use shell architecture as a guide to the conditions of life that, from the point of view of the shell-builders themselves, were instrumental as evolutionary agencies now and in the past. If I were lucky – that is, if the data revealed a discernible signal – I would be able to infer how these conditions of life varied in space and changed through time. Ultimately, I hoped to find a unified explanation based on first principles for the geography and history of life, a comprehensive theory that could also encompass the complexities of the human story.

In this essay, I first describe historical patterns that I believe would emerge in any system characterized by living things competing for locally scarce resources. I then consider the search for patterns and their explanation in the context of an intellectual climate dominated by anti-adaptationist rhetoric and doubts about the validity of scientific approaches to history. Notwithstanding this hostile environment, I present a summary of the economic principles that in my view not only account for historical patterns but also serve to predict future trends and postdict past ones not yet known. A positive feedback between consumers and resources – a historical conspiracy of sorts – implies the existence of inherent directions in the history of living things, including humans. Contingency – randomness and the enduring effects of particular initial conditions and pathways of change – reigns at the level of the precise times, places, order of events, and participants involved in historical sequences. Finally, I discuss why a scientific approach to history is important. By complementing descriptive accounts of the phenomenology of the past, the approach seeks insights into which courses of change are likely and possible and which ones are not. These insights come not from mere parallels of past events with those of the present, but from laws that govern life as it responds and creates inevitable change in a finite world.

Patterns in History

When I was exposed for the first time to living snails in the tropical Pacific in 1968, I noticed that many of their shells were difficult to clean. More often than not, the soft parts of the animal had retracted far into the shell, and the aperture was so small or so narrow that fingers or even needles thrust into the openings were unable to extract these tissues. As I began to observe the diverse predators of these snails, it dawned on me that many features of snail shells – small apertures, tightly fitting rigid doors covering the foot when the body was withdrawn into the shell, the sturdy nodes and ribs on the shell's exterior, and

even the slippery-smooth surfaces of some species – are adaptations that, though imperfectly effective, often thwarted or slowed attempts by predators to crush, hammer, drill, enter, or swallow the shell. These antipredatory defenses were most spectacularly developed in shallow-water marine snails in the tropics, especially in the western Pacific and Indian Oceans, where the predators likewise seemed to have larger or more potent weapons – claws, jaws, suckers, venomous teeth – than those elsewhere.

Contemplating some fossil shells a few years later, I was suddenly struck with the realization that these ancient snails lacked many of the defenses that are so emblematic of tropical shells in today's seas. Shells with slippery surfaces, long narrow apertures, and apertures lined with thickenings around the rim were wholly absent in fossil faunas living more than two hundred million years ago. Architecturally weak shells, by contrast, seemed to become increasingly common the further back in time I looked. Loosely coiled shells in particular were the norm in tropical faunas of Paleozoic times, whereas today they are found mainly in places where shell-breaking predators are rare. These and other observations led me to propose that an evolutionary arms race – a process of escalation between shell-bearing prey and their predators – was responsible for temporal increases in armament among both victims and perpetrators [63, 64].

Once I began to look at other fossils and at the research of fellow paleontologists, escalation and its consequences turned up everywhere. Sea lilies (crinoids), which lived as permanently attached filter-feeders in Early Paleozoic oceans, became mobile, toxic, and spiny as snails, fish, and other enemies became increasingly abundant [21, 38, 53]. Sand and mud on the seafloor at the dawn of animal evolution were essentially free of burrowing animals, but over time they were colonized by many lineages, perhaps as an evolutionary response to predation at and above the seafloor [14, 15, 68]. Burrowers over time penetrated to greater depths and became faster as escalation proceeded apace below the seafloor and as food there became ever more abundant and accessible [58, 59]. These trends, coupled with the evolution of increasingly powerful and mobile predators, made some modes of life untenable. This was the case, for example, for corals and brachiopods that lived unattached and motionless on the seafloor. When extensive burrowing destabilized their mud substrates, these animals would sink into the soft mud and be unable to escape either from such interment or from mobile enemies above [58, 59].

Plants, too, were caught up in the escalatory frenzy. Seaweeds as well as land plants developed all manner of chemical and mechanical adaptations against grazers, and sometimes even came to depend on their consumers for nourishment and successful reproduction [57, 64, 68]. Plant-eaters, it turns out, were late additions to marine and terrestrial ecosystems, a conclusion so at variance with intuition that we delayed publication of our paper on this topic

for a few years until we were quite certain of its validity [73]. A culmination of escalation between plants and their consumers was the Late Cretaceous appearance and mid-Cenozoic expansion of grasses. These plants grow not at the tips, as most plants did and do, but at the base, so that when they are exposed to intense herbivory by grazing mammals (or by lawn mowers), they lose the older, less productive parts of the plant while retaining the ability to grow from less accessible parts of the plant. Grasses and their consumers came to depend on each other [68].

Parallels with escalation between the superpowers were, of course, glaringly obvious. Reading William McNeill's [34] *The Pursuit of Power*, I could not help but be struck by the rapid increases in the potency of weapons through the ages as successive empires varied for world dominance. Escalation, in turn, coincided with an ever increasing per-capita and collective use of raw materials – food, fuel, fiber, building materials – and increases in productivity of those same resources [8]. I was fascinated by these parallels and patterns. Did they reflect fundamentally similar causes? If so, could the history of life tell us something about how human arms races begin and end? Are there inherent directions in history? Alternatively, are these supposed trends merely illusory? Are we simply more impressed by increases in size and might than by decreases?

History as Science and Theory

It was anything but fashionable to ask these questions or even to search for patterns in history. Karl Popper [43, p.143], for example, held that "history is characterized by its interest in actual, singular, or specific events, rather than in laws or generalizations." (Italics removed.) In a similar vein, Stephen J. Gould [25, p. 25] doubted the existence of patterns and discouraged the search for them: "The history of life is a story of massive removal followed by differentiation within a few surviving stocks, not the conventional tale of steadily increasing excellence, complexity, and diversity." The intellectual climate of the late 1970s through the 1990s was dominated by the ascendant view that chaos and randomness were the predominant themes of history. Many paleontologists were influenced by Gould and Lewontin's [26] view that adaptation was at most a temporary, ephemeral phenomenon whose effects on the history of life paled into insignificance in the face of periodic mass extinctions and the stranglehold of unique, and therefore unpredictable, initial conditions and coincidences. Perhaps snails and their predators engaged in evolutionary escalation [24], but such patterns and processes could not possibly be the rule in a world dominated by chaos. Even the cherished idea that complexity increased through time – the one pattern of history that still held sway among diverse scientists [1, 4, 6, 37, 56, 61, 80] came under attack as

scientists realized that many stocks decreased in complexity and probably outnumbered those that increased in complexity [35, 36].

The atmosphere of the time was aptly captured by Gould's [25] metaphor of the tape of life. Following a similar point made by Simpson [54], Gould held that if the tape of life – the sequences of events comprising life's history – were run twice, the outcomes would be radically different. Initial conditions – ancestral states, the particulars of time and place – put an indelible stamp on subsequent events, participants, and pathways of change. Even if we knew the points of departure, there would be many other chance events and forks in the road along the way, with the result that directions of change would be unpredictable and the search for causal historical patterns would be futile. The only predictable patterns would be inherent in the dynamics of evolving lineages – origin, splitting, and disappearance – that would be independent of time and place. This so-called nomothetic approach [45] led many paleontologists to treat taxonomic and phylogenetic units as abstract entities, which could be counted and modeled without regard to their environments or interactions.

The abstraction of nomothetic paleontology matched in spirit what biologists who were trying to reconstruct ancestor-descendant relationships were doing. For these so-called cladists, the construction of evolutionary trees involved morphological (and later molecular) characters, which were taken as abstract markers of descent from ancestors. Functional aspects of these characters were intentionally ignored or excluded because they were judged to be unreliable indicators of descent.

The combination of nomothetic paleontology and "tree-thinking" led to the emergence in the 1970s of a macroevolutionary interpretation of the fossil record. Macroevolution is concerned not with the behavior of individual organisms and their interactions, but with the birth, growth, decline, and death of inclusive taxa (genera, families, orders, etc.) and later of clades. A clade, defined as an ancestor and all of its descendants, has properties – geographic range, number of species, propensity for genetic isolation of populations – that individual organisms do not have. These emergent characteristics, so the thinking goes, differ among clades, and influence the probabilities and rates of species formation and extinction. Phenomena that affect whole populations thus impose a kind of sorting among clades [16, 23, 74-77].

The macroevolutionary worldview in its purest form implicitly assumes the null hypothesis that clades are internally homogeneous. Within a given clade, all members are subject to the same adaptive limitations, live in comparable habitats, have comparable modes of life, have similar life histories, and are therefore interchangeable. The clade therefore has time-invariant emergent properties, or at least potentials, throughout its evolutionary history from origin to extinction.

We know, however, that this null hypothesis is false for most clades. The Rhynchonellata (the formal name of the clade that contains the vast majority of brachiopods, bivalved suspension-feeding animals commonly known as lamp shells) comprise a hugely diverse group of animals. During the Paleozoic and to a lesser extent the Mesozoic era, they occupied a wide range of marine environments, ranging from shallow tropical reefs and sand-flats to cold waters at high latitudes. Some Late Paleozoic species became large, fast-growing reef-formers whose competitive dominance in those environments derived from the likely presence of photosynthesizing symbionts in their tissues [10]. Today, the few hundred brachiopod species are uniformly slow-growing, low-energy animals confined to cold or cryptic habitats, where they tend to be subordinate to such other suspension-feeders as true bivalves (clams), barnacles, and sponges. Not only has the clade contracted ecologically from mid-Mesozoic times, but much of the heterogeneity of its Paleozoic and Mesozoic members has been lost. By contrast, the Arthropoda (the animal clade including crabs, spiders, and insects) initially consisted of small to medium-sized marine predators, swimming suspension-feeders, and sediment-ingesters. Later it gave rise not only to land animals, including herbivores and social insects (ants, bees, wasps, termites, and bark beetles), but also to my favorite group, the barnacles, sedentary crustaceans whose external mineralized shells converge in their mode of accretionary growth on the shells of molluscs. These clades are internally heterogeneous in every imaginable dimension of morphology, life history, habitat type, geographic range, power, competitive status, adaptive syndrome, and time. A clade is a branch of the tree of life, and nothing more; the characteristics of its founding member have long since been transcended as opportunities arise and as extinction prunes branches and twigs within the clade.

A worldview of human history that would resemble the macroevolutionary perspective on the history of life is an emphasis on the genealogy and replacement of rulers or institutions. For example, we might compare patterns of descent and replacement among the French, English, and Spanish monarchies. Knowing such sequences of the makers of history is indeed essential, but neither the details of genealogy nor an inventory of the wars in which these rulers engaged or the countries these rulers conquered or lost suffice as descriptions or explanations of history.

Neutral theory extends throughout population biology, from genetic mutation to the distribution of individuals and species [29]. Under the null hypothesis of neutrality, outcomes and patterns are determined by chance, with deterministic factors either absent or canceled out. Because the units of interest are effectively interchangeable, their names and roles are superfluous and irrelevant, and their heterogeneity can be ignored. Such a null model may indeed describe the observed behavior of genes, individuals, and species in space and time, and it may be a useful point of reference against which to

measure the properties of real systems and their constituents [29]; but it must never be construed as an explanation for the behavior of living things and the structures they produce. Living things are agents of change whose interactions have outcomes that affect their own fates and those of other organisms. Chance and randomness are therefore insufficient agencies for capturing even the fundamentals, let alone the particulars, of living systems.

If neutral theories and unadorned chronologies of events do not suffice as historical explanation, how do we gain a coherent understanding of history without being overwhelmed and distracted by the details? In my view, we need a theory of history that incorporates the unique, emergent properties of living systems. The theory must explain the causes, effects, feedbacks, and conditions that create the sequences of history. It must predict general patterns of change under all the conceivable circumstances in which metabolizing life is sustainable, but not the times, places, or precise sequences of events. In short, a theory of history must be like the theory of forces in physics in that it circumscribes outcomes when initial conditions are specified and rules of interaction are applied. It must explain variations in the realization of laws in space and time according to circumstances at levels of inclusion ranging from the ephemeral and local to the timeless and global. The interactions must have consequences for the fates of the living entities involved, fates influenced by the environment and by structural properties of those entities. For living things, these interactions and outcomes are economic, with the performance of participants influencing survival and propagation.

This approach is thus a scientifically grounded history of function as influenced by structure rather than a history of structure alone. Patterns and trends must be expressed in terms that are meaningful to the lives, fates, and relationships of living things. I thus prefer the language of adaptation, activity, metabolism, interaction, and performance – all carefully defined, measured, and compared – over the language of diversity, complexity, and information. These latter, more abstract concepts are epiphenomena, manifestations of the more fundamental, function-based properties and capacities that rule organisms' lives. There is, of course, a history of complexity, diversity, and information. In fact, both complexity and diversity appear to have increased over the course of Earth history as well as in the long-run history of humanity. These trends reflect more basic economic changes, which are the product of evolution and the distribution of power in the biosphere.

But theory, too, was anathema to many historians. Popper [43, p. VII] maintained that "There can be no scientific theory of historical development serving as a basis of historical prediction." For him, "the evolution of life on earth, or of human society, is an unique historical process" (p. 108). Unique phenomena can be described, and take place in accordance with the laws of physics and economics, but by virtue of their uniqueness are neither available for application of scientific tests nor the basis of a scientific theory. Berlin, too,

saw a profound distinction between history and "natural science," by which he mostly meant physics and chemistry, disciplines with timeless laws, forces, and structures. Indeed, he considers a scientific approach to history a fool's errand: "Whereas in ... developed natural science we consider it more rational to put our confidence in general propositions or laws than in specific phenomena ... this rule does not seem to operate successfully in history" [3, p. 111]. In the same vein, "Historical explanation is to a large degree arrangement of the discovered facts in patterns which satisfy us because they accord with life ... as we know it and can imagine it. That is the difference that distinguishes the humane studies – *Geisteswissenschaften* – from those of nature" [3, p. 132]. Berlin ascribes to historians, but not to scientists, "a capacity for integration, for perceiving qualitative similarities and differences, a sense of the unique fashion by which various factors combine in the particular concrete situation ..." [3, p. 140]. In other, more modern words, Berlin saw natural science as reductionist, and history (by which he meant almost always human history) as incorporating synergies and emergence, interactions and organization of parts that create wholes with properties and interactions different from those of component parts. Like Popper, he did not conceive of historical science as real science, reducible to elementary particles and forces.

I believe these distinctions between science and history are far too starkly drawn by these critics. If we applied Popper's and Berlin's logic to the behavior of individual molecules, rocks, continents, stars, or galaxies, we would have to clear away all the particulars to discern the reduced laws of physics and chemistry, yet these laws apply just the same. The behaviors of objects, like the interactions of living things and the conditions in which those interactions take place, are realizations of those laws. General patterns can emerge despite these particulars if certain sequences are more likely than others, and if classes of interaction have predictable outcomes on the basis of measurable properties. The trends are statistical directions, not strictly deterministic; they emerge from simpler components and simpler interactions, much as complex wholes with new properties emerge from interactions among their parts. The fundamental methodology is comparative and systematic [12, 22] rather than strictly experimental, that is, historians must draw inferences from given circumstances rather than from ones they can manipulate. The scientific approach to history entails testing hypotheses with as many independent sources of evidence as possible, set in the framework of a unified explanatory theory. History is at once reductionist and holistic, concerned with elementary principles as well as with the new properties that emerge when circumstances and the things in them work together and effect change.

Although the view of history that I have come to embrace emanates from the world of plants and animals, I believe that this scientific approach is just as powerful in human history. True, studies of human affairs are apt to emphasize motivations and emotions of individuals, attributes that likely do not figure

prominently in the lives of most other organisms; but motivations and emotions reflect real circumstances, or at least circumstances as people perceive them, and are therefore as important to understanding human relations as sexual selection and predation are to interaction among, say, butterflies. It is also true that historians value narrative over any kind of theory-laden approach. For them and for like-minded paleontologists, it is the particulars of a situation that are the primary focus of study. But if we are to learn from history, narratives must be placed in a broader context of comparisons among places, among times, among social settings, and so on. I agree with Gordon Wood [78, p. 6] that "History ... may not teach us particular lessons, but it does tell us how we might live in the world." History can do this only if its narratives collectively reveal limitations and possibilities and if they identify pathways of change that are likely and those that are improbable. Comparisons undergirded by a unified scientific theory of history and by hypothesis-driven methods of investigation will, I think, yield the deepest and most useful insights. Studies by Diamond [12, 13], Pomeranz [42], and Clark [7] exemplify the power of this approach well. In short, historians need the principles of interaction that economists and evolutionary biologists have identified, together with systematic methods to construct a chronology of the past.

An Economic Theory of History

History consists of events, conditions, pathways, and participants arranged in temporal sequences. The patterns of history, which we must describe, are linear sequences – one thing following another – that not only branch (or divide), as in a phylogeny (ancestor-descendant relationships), but that interact by exchanging resources, energy, or information. Mathematically, these patterns are best expressed in the language of topology – connectedness in networks, patterns of branching, and transformations of geometrical configurations – and by the use of matrices in which the individual cells represent strengths and signs of interactions. This language accurately reflects the central importance of interactions in creating pattern [66].

But description, even if it is done in precise mathematical language, is not explanation. Essential though it is, description represents only the first step in historical inquiry. History is about causes and effects, about how supply and demand are connected through feedback, about how disruptions affect systems, about how circumstances act together to create or favor new states, and about whether an arrow of time is discernible among the billions of historical sequences that seem so dominated by the particulars of time and place. For living things that depend on resources for survival and propagation, interactions are economic in nature, involving the distribution of a multitude of primary essentials and secondary requirements. Life's metabolism, in other

words, implies an explanation of history founded on principles of competition, cooperation, production, consumption, and trade.

Organisms do the work of life – maintenance, growth, reproduction, and adaptation – by harnessing energy and matter through the processes of synthesis and metabolism. Whenever two or more living things attempt to acquire the same resource at the same time and place, the resource will be locally scarce, and the organisms involved will compete for it. The competitive position of living things in the system of which they are a part is determined by the performance of individuals in acquiring or retaining resources. Economic performance is best expressed in units of power (energy, or work, per unit time). Resources are the currency of the system; they can be gained, lost, stored, exchanged, and spent. Success – persistence and the ability to propagate – requires sufficient resources, but does not strictly depend on performance.

A resource like food, shelter, and water (for land organisms) becomes a target of competition among individual living entities when it is locally scarce and when it influences the survival and propagation of competitors. Local scarcity, however, applies only to the competitors themselves, not necessarily to the population to which the competitors belong. For example, animals as a group are not limited by the amount of oxygen in Earth's atmosphere, but oxygen may be in critically short supply for two mammals sharing the same underground burrow. A resource may therefore not limit the size of a population even though at the scale of interaction between individuals it is locally scarce and therefore a target of selection [65, 72]. Evolutionists concerned with selection are therefore apt to view competition and resources differently from ecologists, because the former are concerned with individual interactions whereas the latter deal with phenomena at the population level. Even so, local scarcity and population-related selection occur in the larger context of populations and ecosystems. The availability and accessibility of resources at the population level therefore affect the extent to which individuals can compete for, adapt to, and influence the locally scarce commodity.

A competitive interaction is almost always unequal in its outcome for the participants, with one party gaining more or losing less resource than the other. The winner gains an economic advantage not only in acquiring the contested resource, but also in gaining access to environments where the resource is plentiful and accessible. The loser is economically marginalized or, in extreme forms of competition leading to starvation or predation, eliminated.

Within a system of competitors, the entities with the greatest individual or collective power exert a disproportionately strong influence on the phenotypes, activities, distribution, and resources of the living things with which they interact. Because of intense competition among them, these dominant entities therefore exercise intense selection among subordinates as well as among their

fellow dominants. In this view, selection is due largely to enemies, and is a predominantly top-down process whose intensity and effects are proportional to power. The universally observed inequality in performance in competition among individuals and in the distribution of resources thus spreads and amplifies through the entire system [68].

The maximum power available to a dominant competitor increases as resource availability and accessibility at the population or ecosystem scale increase. The scope of adaptation – that is, the range of adaptive possibilities available to an evolving lineage – and the maximum level of performance are higher when the population-level supply of resources is plentiful and predictable, when the system in which the population is embedded is large (enabling a population of rare but metabolically active individuals to sustain itself in the face of chance fluctuations), when temperatures are high (reducing the activation energy required to initiate energy-consuming processes), and when the organism has the chemical and mechanical equipment to locate, acquire, and hold resources [66, 68]. These conditions are satisfied for terrestrial organisms on large, warm, well-watered, productive land masses; and for marine ones in large, warm bodies of water with high inputs of nutrients from the land or from deep-water sources. Power, performance, and the conditions for the enhancement of energy-intensive traits associated with competitive dominance and with escalation are thus most favorable when the economy of life grows, that is, when productivity and temperature – the enabling factors of an economy – rise [67].

Power, performance, and the scope of adaptation are constrained when resource supply is low and unpredictable. When the economy in which a population operates is small, as on isolated oceanic islands or in island-like habitats such as lakes, very small populations are prone to extinction and cannot persist for long. To maintain a viable population, therefore, individuals in such small habitats must have relatively modest metabolic requirements, because with high per-capita demand the limited available resources can support only a small number of individuals. Power is also limited in organisms that maintain body temperatures similar to those of the environment when conditions are cold, as in today's polar regions and the deep sea. From the dimensionality of power, it is clear that many pathways toward greater competitive performance are available to living things. These include increases in body mass, applied force, velocity, rate of growth, metabolic rate, and cooperation, as well as decreases in the time of exposure to enemies. Still another pathway to greater performance is the ability to interfere behaviorally or structurally with the performance of rivals.

Given that a top competitor has to perform many functions well, it is not surprising that cooperation and other forms of interdependence rank as perhaps the most important means for enhancing the competitive ability of organisms. Most, and perhaps all, organisms are composed of parts that work

seamlessly together but which have separate evolutionary origins. Familiar examples are the eukaryotic cell, whose organelles – mitochondria, plastids, and basal bodies, among others – were initially free-living prokaryotes of diverse origin that formed an intimate partnership with another prokaryote bearing what we now recognize as the nucleus; and land plants, which effectively tap nutrients from the soil by virtue of symbiotic fungi in their roots. In such integrated partnerships, the various components perform complementary functions, which collectively enable the emergent individual to perform better as a competitor than any of the components could by themselves. Other forms of cooperation, often associated with division of labor among individuals, lead to colonial animals, insect societies, group-hunting dogs, and human society. Flowering plants have in many cases come to rely on highly mobile pollinators to facilitate sexual reproduction, and therefore need no longer grow close to each other as they do when pollination is by wind or water. Specialized herbivorous insects therefore perceive their hosts as rare, meaning that insect- or bird-pollinated plants can achieve a measure of protection from their enemies and can instead devote more of their budget to rapid growth [28, 30, 31, 47]. The plants themselves, and the ecosystem of which they are a part, therefore achieve higher productivity when they form these intimate partnerships than when they work independently as self-sufficient entities [32]. Interdependencies, in other words, are created by, and in turn further promote, the evolution of competitors.

In the light of these arguments, it should come as no surprise that the most highly escalated species have arisen in the competitively most rigorous situations. Tall, competitively dominant trees are the evolutionary products of continents, not islands. So are weeds – fast-growing plants with prodigious fecundities and short life-spans – and social insects. The most potent and the most heavily armored marine animals evolved in the Indo-West Pacific region, and humans emerged in Africa, not in the much more island-like continents of South America or Australia. In the human realm, civilizations tend to spring up where marine resources are abundant and where equable climates and high diversity have favored the evolution of plants and animals that humans could successfully domesticate [12].

Competitively subordinate entities vastly outnumber dominants in both individuals and species. Many of them nevertheless evolve toward greater power because of selection due to their enemies. Others succeed in situations where power requirements are low and where resources and enemies are scarce. Such situations include life on or in the bodies of other living things, occupation of cluttered environments, physically hostile habitats such as wave-swept sandy beaches or wind-swept mountaintops, and nutritionally starved environments such as caves or the abyssal plain of the deep sea. Importantly, competitively vigorous species often create situations suitable for subordinates: tall trees cast shade, in which competitively subordinate plants

can thrive; fast-growing reef corals, powered by photosynthesizing single-celled algae in their tissues, create numerous crevices and cavities where thousands of small-bodied animals make a living; and the bodies of well-defended plants and animals are inviting targets for vast numbers of parasites and symbionts, which would be highly vulnerable to enemies if they were free-living.

Disruptions affect all systems from time to time. Production, consumption, and escalation are interrupted when catastrophes, often originating outside the sphere of life, disrupt patterns of interdependence. Extreme episodes of disruption in the biosphere are recorded as global mass extinctions, such as those marking the termination of the Paleozoic and Mesozoic eras (the end-Permian and end-Cretaceous extinctions respectively). These episodes may have begun as crashes in production of food by plants and plankton, brought about by collision of Earth with extra-terrestrial bodies and by enormous volcanic eruptions leading to the formation of vast tracts of basalt. The initiation disruption propagated throughout the biosphere, destroying the collective regulation of the resources that remained and creating conditions in which many populations became inviable either because of starvation or overexploitation by consumers [50, 51, 69]. In the realm of recorded human history, climatic change – droughts, volcanically induced cold rainy summers – caused crop failures, which together with a pervasive tendency for technologically sophisticated humans to overexploit natural resources for food and fuel appear to be instrumental in bringing about the collapse of civilizations that, like ecosystems, are built of highly interdependent relationships among individuals [13, 41].

Feedbacks, Cycles, and Trends

Through selection and their own metabolism, living things formulate and test hypotheses of their changing environment, which consists of enemies, allies, resources, and disruptions. They respond (and therefore adapt) to their environment, but they also change their surroundings, and therefore take an active role in creating the circumstances in which they live. The good fit between organism and environment that impresses most naturalists therefore results from a feedback, in which living things and their surroundings influence each other. An organism – its form, activity, physiology, and life cycle – thus represents an integrated system of adaptations reflecting supply, demand, and construction. It is a web of synergy, of interdependence in which resources, metabolism, competition, and structure are inextricably linked through causal feedbacks. Similar statements apply to life at all levels of organization, from the cell to the ecosystem and beyond, as well as to the human realm. The material manifestations of life differ among levels – an ecosystem and a society consist of multiple individuals, whereas organisms

and cells are integrated indivisible units – but the feedbacks and interdependencies that make life sustainable are universal [9, 68].

One example will illustrate this point. Hermit crabs are crustaceans that typically inhabit the abandoned shells of snails. Even when shells are abundant, most are occupied by hermit crabs. As a consequence, hermit crabs compete intensely for shells. Because shells deteriorate when occupied by these crustaceans, the hermit-crab population depends on a supply of new shells to remain viable. In some environments, such as freshwater streams, shells become available episodically, especially following floods. Most of the time, therefore, the supply of suitable shells is low, but a few times a year, or perhaps every few years, there is a surplus. This regime of supply is too unpredictable to sustain a population of hermit crabs or other secondary shell-dwellers; and indeed such shell-dwellers are mostly unknown in freshwater ecosystems. In the sea, predators that leave the shells of their snail victims intact are often numerous. Because they must eat year-round, especially in the tropics, they provide the population of hermit crabs with a more or less constant, predictable supply of shells. This regime of supply, regulated by the predators of snails, thus allows animals like hermit crabs to exploit the resource of shells for mobile shelters, a form of specialization that is strongly selected for by abundant predators on and above the seafloor. By effectively lengthening the life-span of shells, the hermit crabs greatly increase the abundance of shell-bearing animals as a potential resource for predators. In so doing, they increase the population and potentially the power of predators, and thus indirectly increase the benefits of occupying well-armored shells.

Neither these feedbacks nor the evolution of high-powered competitors is possible without enabling factors, which comprise resources and the factors that make those resources available, accessible, and predictable to consumers. If the supply of resources were controlled entirely by extrinsic factors – that is, by disruptions or chronic constraints beyond the control of living things – the maximum power achieved by successive dominants and by the system as a whole would fluctuate according to the pattern of supply, but it would not show a generally upward trend. If, however, there were a strong positive feedback between resources and consumers – that is, if high-powered consumers and the system as a whole promote the productivity of resources – and if permissive conditions favoring such feedback are more prevalent than constraining ones, there should on average exist trends toward increasing power among dominants as well as in the systems in which they live. These possibilities prompt a fundamental question in history. Are there trends in performance that transcend the effects of disruption and other conditions beyond life's control, or are disruptions so frequent and so severe that all advances in power, reach, dependency, and regulation are canceled out or even reversed? I believe that long-term trends toward greater power are in fact observable both in human history and in the sequences of nonhuman life,

implying a reduction in the effects of extrinsic variation in enabling factors. By establishing a positive feedback between competition and resources, life therefore unintentionally imparts an arrow of time to history.

The repeated occurrence of disruptions has led many historians to view history as a succession of cycles. Following a disturbance, the cycle begins with an episode of renewal and growth, followed by a phase of established maturity, and again terminated by a disruption. Cyclical behavior, often with a very regular periodicity, has been claimed for mass extinctions [46], astronomically forced climate [11, 19, 40], continents coming together and drifting apart [18, 60, 79], diversity [19, 49], empires [5], ocean chemistry [33, 48, 52], flood-basalt volcanic eruptions [44], and prices [25]. Strict periodicity has been disproved for all cycles except astronomically forced climate.

Conditions favorable to the evolution and maintenance of interdependence and powerful competitors should be far more common than disruptions, implying that systems of life should exhibit long-term trends toward greater power and productivity. High-powered competitors are at a disadvantage, and interdependencies break down, only during disruptions, which by definition are infrequent, temporary, and episodic. Competition, on the other hand, is universal and relentless, and tends to favor entities with greater power. The high demand of dominant competitors both requires and promotes high turnover (and therefore high productivity) of resources. Moreover, interdependencies stabilize resource supply and stimulate the biological equivalent of trade. Under permissive conditions of increased extrinsic inputs of accessible material and energy resources, intense competition and interdependence create opportunities for the establishment of energy-intensive innovations, which further stimulate demand and therefore supply. Although permissive conditions are likely to be just as infrequent and episodic as are disruptions, the advantages of power and interdependence apply even when the delivery of resources is constant. Increases in power and productivity are likely to be difficult or impossible under such conditions of resource stability, but the maintenance of high levels of consumption and production is unaffected. Reversals are thus limited to times of disruption, whereas growth and maintenance prevail at all other times [67, 68].

To some authors, the constancy or reduction in power that subordinate entities experience over evolutionary time count as much as do increases in power, and therefore contradict any long-term trend toward increasing power. I maintain, however, that increases have a much greater effect on the selective regime in the larger system than do decreases [71], because a system's productivity and rate of consumption are determined largely by its competitively dominant members. The removal or addition of high-powered producers and consumers has far more dramatic effects on the pattern of selection and on the web of interdependence than does the removal or addition

of a low-energy entity. Accordingly, more weight must be given to increases in power than to decreases.

Studies of geochemical cycles of essential inorganic components of life – oxygen, carbon, silicon, calcium, phosphorus, nitrogen, and water – indicate a trend of increasing biological control over these resources through time. These controls are temporarily interrupted during times of mass extinction, but they are quickly re-established during recovery. Increased biological regulation is made possible by dominants with higher metabolic rates, which speed up rates of turnover and therefore productivity of communities. Patterns of trade or subsidy between adjacent systems (land and sea, shallow and deep water, above and below ground) increase as new, faster modes of consumption evolve and as animals become more mobile. Economic dominants owe their competitive success in part to activities and characteristics that "help" entities with which they interact. Cooperation represents a particular effective version of this "help", but consumers also have many indirectly stimulatory effects on the conversion and recycling of resources for use by organisms.

These long-term trends have persisted despite substantial disruptions. The same is true for the diversity of species in the sea as well as on land [2, 27, 55], per-capita energy use by humans [8], and all escalation-related trends [68]. The available evidence thus indicates that, despite the imposition of cyclical phenomena by disruptions, the history of life is dominated by long-term trends toward increased power, productivity, interdependence, and regulation.

Concluding Remarks

The particulars of history – participants, dates, events, and places – cannot be predicted and remain profoundly contingent, but production and its regulation by consumers conspire to give history a predictable direction of increased power and reach of dominant members of living systems. This directionality is an emergent property of living systems, inherent in the interactions and competitors, consumption, and resources.

The identification of directionality in history has led some authors to postulate the existence of some supernatural driving force. Wright [80, p. 323], for example, argues that biological evolution has “an arrow – the invention of more structurally and informationally complex forms of life” and that “this arrow points toward meaning...” This “isn't, of course, proof of the existence of God. But it's more suggestive of divinity than an alternative world of directional evolution but no consciousness.” Conway Morris [39] expressed similar sentiments. I emphatically reject such speculations. Directions and patterns emerge entirely through the interactions of components and circumstances, and need no supernatural force or being.

The ability to reconstruct the past and to explain historical sequences in terms of scientific laws is surely one of the great triumphs of the collective

human intellect. The challenge before us now is to use these historical insights the chart the right course for our collective future.

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