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Introduction

OPABINIA WAS only a few inches long, with about 15 paired, undulating flaps on the sides of the body, a head with five bulbous eyes, and a long, flexible proboscis ending in a pair of spiny claws. Long one of the weird wonders from the 505-million-year-old rocks of the Burgess Shale in western Canada, the few specimens of *Opabinia* are now known as part of an evolutionary burst leading to arthropods in the Cambrian Explosion of animal life. Finding a home for *Opabinia* among the arthropods makes it no less remarkable. If anything, it sharpens our questions about the processes that generated such remarkable evolutionary novelties.

Evolutionary novelties abound. Consider grasses. Grasses have been supremely successful, with grasslands carpeting the temperate interiors of North and South America, Asia, and Africa for the last 15–20 million years. Grasslands changed the structure of terrestrial communities, modifying regional climate, and stabilizing soils against erosion, probably even reducing the sediment flowing down rivers to the oceans. Studies of the fossil record of minute silica particles (known as phytoliths) in grass stems by paleobotanist Caroline Strömberg, coupled with molecular evidence, show that grasses originated 55 million years ago, or perhaps earlier. From their widespread success one might assume that grasses spread soon after they first appeared. Yet grasses were ecologically insignificant for tens of millions of years before changing climate accelerated a pervasive change in terrestrial ecosystems. So, grasses originated and diversified into their major clades long before they became ecologically or evolutionarily successful.[1]

Similar lags have long been recognized between invention and the impact of a new technology. Although patent records are often used to study new technologies, most patents have little economic impact, and there is often a lag between discovery of a new technology and the onset of a significant role for it in the economy. The complexity of technological innovation is illustrated by the early history of digital computers. Over the winter of 1937–1938 John Vincent Atanasoff, a physicist at the Iowa State College, built the first digital computer to speed up laborious calculations. His computer was not programmable, but like modern digital computers it solved complex equations using Boolean logic and binary numbers. Although Atanasoff is often credited as the inventor of the digital computer (and eventually won recognition in a patent suit), the spread of digital computers was due to the development of ENIAC (Electronic Numerical Integrator and Computer) in 1943–1944 at the University of Pennsylvania (some of Atanasoff's ideas may have found their way into ENIAC, but that is a story for another day). As ENIAC was being built, British codebreakers at Bletchley Park were building Colossus, a fully digital computer, to help solve German codes. Atanasoff's computer was discarded as scrap at Iowa State, and the existence of Colossus would remain secret for decades, leaving ENIAC as the first fully digital, programmable computer. More importantly, some of the builders of ENIAC founded a company that became part of the Sperry-Rand Corporation and the beginning of the digital revolution.[2]

The importance of such lags is best illustrated through a brief look at three approaches among biologists since Darwin published *The Origin of Species* in 1859.

Darwin argued for a continuity of evolutionary processes from small-scale changes observed in living plants and animals to the longer-term patterns revealed by the fossil record. By denying the discontinuities suggested by some earlier natural scientists, Darwin emphasized the power of natural selection to explain the diversity of life. Although most scientists quickly accepted Darwin's views of descent with modification, natural selection was only one of many explanations debated in the interval between 1860 and the 1930s, in part because of controversies over how organismal attributes were passed to the next generation. These controversies were seeming resolved by geneticists and evolutionary biologists in the Modern Synthesis of evolutionary biology (1920s–1950s). Many contributors to the Modern Synthesis adopted Darwin's extrapolationist approach, updated with the recent discoveries in genetics. Paleontologist George Gaylord Simpson and evolutionary biologist Ernst Mayr focused on the origin of larger groups as a proxy for evolutionary innovation. For example, from this perspective the critical issue in the origin of turtles was the vertebrate order Testudines, which encompassed their morphological novelties. Mayr viewed evolution as opportunistic, capitalizing on useful morphological novelty, while Simpson beautifully articulated the variety of evolutionary patterns documented by the fossil record (his 1944 book *Tempo and Mode in Evolution* remains an intellectual touchstone for paleontologists). By the 1950s Simpson had adopted the reigning views of the Synthesis, that natural selection could, over time, craft the full panoply of the history of life. This extrapolationist view, that selection at the level of individuals within populations via small changes in genes, is, over time, responsible for remarkable evolutionary novelties, has long been the default assumption by evolutionary biologists and viewed as immune to deeper inquiry.[3]

A second approach to novelty extends the extrapolationist view. Confronted by new opportunities a species may diversify into a range of new species, each specialized for different opportunities—food type, habitat, and so on. Simpson explored these adaptive radiations from the 1940s to the 1960s, extrapolated from living plants and animals, often on islands, to more complex diversifications such as the spread of placental mammals and even the Cambrian Explosion of animals. In 1960 Simpson wrote: "On a broader scale, we now see, even more clearly than Darwin did, that every marked expansion of a group, whether it be a genus or a phylum or the whole animal kingdom is an adaptive radiation."[4]

Subsequent generations of evolutionary biologists have examined adaptive radiations, including Darwin's finches in the Galapagos Islands, repeated invasions of small marine fish into lakes in British Columbia, and the remarkable expansion of the *Anolis* lizards across the Caribbean, establishing them as important contributors to diversity. But the theory of adaptive radiation assumes that the generation of new morphologies is a sufficiently regular occurrence that we do not need to worry about the supply side of the equation. The hinge point is the ecological opportunities that facilitate the radiation, whether migration to a largely unoccupied island, the aftermath of an extinction, or the acquisition of a "key innovation" that allows access to new resources. But the significance of adaptive radiations for morphological novelties seems limited, since few are associated with adaptive radiations. In later chapters evidence for lags between the origin and success of novelties will support the distinction between novelty and innovation. Moreover, these chapters reveal that not all novelties are a response to an opportunity or need.

Extrapolationist views invoke the principle that explanations with the fewest assumptions should be favored over more complex scenarios. Known as Ockham's razor, this principle of parsimony is attributed to William of Ockham, a medieval English monk. Isaac Newton made similar arguments, writing in his *Principia*: "Nature does nothing in vain, and more causes are in vain when fewer suffice. For nature is simple and does not indulge in the luxury of superfluous causes." Darwin had enough challenges arguing for the evolutionary unity of life and for the power of natural selection in crafting biological diversity without multiplying the range of processes. Similarly, advocates of the Modern Synthesis were trying to consolidate evolutionary biology through the incorporation of field natural history, genetics, and the fossil record, which also favored extrapolating from selection within populations. Thus, neither extrapolationist nor adaptive radiation scenarios for the origins of novelty and innovation can be rejected out of hand. The assumptions made by Simpson, Mayr, and their colleagues were reasonable, particularly as they were working to produce a more scientific view of evolutionary change. In fact, elements of them may make important contributions to a broader understanding of these problems. But nonetheless they seem to fall short of a full and comprehensive understanding of the phenomena of novelty and innovation.[5]

The third, more recent, approach reflects growing experimental evidence that new morphologies often reflect different sources of genetic variation from those fueling adaptation. New molecular methods of interrogating the genes and gene networks responsible for development from an embryo to an adult have revealed a remarkable and unexpected conservation of genes across many kinds of animals. Hox genes, involved in animal patterning, and *Pax6*, responsible for eye development in vertebrates, have become broadly known, but there are many more. From the extensive conservation of these genes among living animals we can infer that their last common ancestors also possessed these genes, even if the genes may have had somewhat different roles. These discoveries have led to the rise of comparative evolutionary developmental biology, or "evo-devo." The origins of novel attributes of animals (and some plants) have attracted considerable attention and have suggested the need for an expanded view of the origins of novelty.

While the classic model of an adaptive radiation involving a "key" morphological innovation assumes a close connection between the origins of novelties and their evolutionary success, there is no logical or necessary connection between the two phenomena. To Mayr the suggestion of a lengthy gap between the origin of a morphological novelty and its ecological or evolutionary success would seem nonsensical, if not bizarre. Mayr focused on the origin of higher taxa as a metric of evolutionary novelty, but novel morphological features often define new clades, and a new clade, whether turtles, grasses, or birds, involves the assembly of a suite of features. The evolutionary history of grasses illustrates that the innovation associated with a clade may be decoupled from the attributes that define the origin of the clade. But evolutionary developmental biologists are in some ways the reflection of advocates of adaptive radiations, for they emphasize the mechanisms that generate novel forms but often neglect the problem of how these new forms succeed and make a living. The origins of novelties, innovations, and clades are distinct issues. They may occur simultaneously, as Simpson and Mayr assumed, but that is a question to be resolved by study of individual cases, not assumed.

Distinguishing the origin of novel forms (novelty) from their success (innovation) is critical to understanding the processes responsible for their formation. I will define these terms more carefully later in this book, but for now we can treat the origin of novelty as the formation of unique features: the carapace of a turtle, the growth habits of grasses, feathers and skeletal changes for birds, language for humans. In contrast, innovations involve transformations of ecological assemblages and long-term evolutionary impact. Innovations are often more complicated than simply the acquisition of a morphological novelty, for they reflect the ecological and evolutionary success of a group, which may require additional adaptations beyond a novel morphology or environmental changes, as was the case with grasses.

The spread of evo-devo has led many biologists to reexamine the driving forces for novelty and innovation, informing the three major issues explored in this book: *How did novel attributes arise, and how did they become successful innovations? Can the same general model explain novelty and innovation across biological, cultural, and technological domains?* Finally, *does novelty simply represent the extremes of adaptive evolutionary change, the sort of thing that happens every day, or are novelty and innovation somehow decoupled from evolutionary adaptation?* As a foundation for what follows it is worth briefly elaborating on these three questions.

No comprehensive account of novelty and innovation in the biological domain can focus exclusively on genetic and developmental changes, on ecological opportunity, or on changes in the environment, any more than a useful account of technological change can focus on inventions to the exclusion of their economic success or failure, or an account of cultural innovation can ignore the broader context in which the changes occur. Exploring the origin of novelties and innovation constitutes chapters 6 through 9, with numerous examples in other chapters as well.

Novelty and innovation have become popular themes in evolutionary biology, business, economics, and culture, among other fields. Biological novelty, evolutionary innovation, cultural transformation, and technological change are usually treated separately by evolutionary biologists, anthropologists, and economists. There is a widely shared (if sometimes a bit inchoate) view that there are great similarities among biological, cultural, and technological innovation. But rarely has the nature of such similarities been investigated in detail. Yet human language, culture, and technology represent some of the most transformative novelties in the history of life. This motivates the second major theme of this book: *Can the same general model explain novelty and innovation across biological, cultural, and technological domains?* If a general approach to novelty and innovation is possible, it must encompass culture and technology.[6]

Charles Darwin famously drew upon the work of Thomas Robert Malthus as inspiration for his theory of natural selection. Modern evolutionary biology and modern economics trace their intellectual history back to the field of political economy in the eighteenth and early nineteenth centuries through Malthus, Adam Smith, Nicolas de Condorcet, and others, with continuing intellectual cross-pollination. Many economists have been deeply influenced by work in evolutionary biology. Economist Joseph Schumpeter has often been credited with distinguishing between invention and innovation in the evolution of technology. Schumpeter was a leading twentieth-century theorist of economic development and entrepreneurship. He emphasized the importance of technological innovation but recognized that inventions by themselves contributed little. It was only when inventions diffused through an economy that they could became innovations and influence economic growth. Just as I view Schumpeter's distinction between invention and innovation as equally applicable to the history of life, I will introduce other approaches from economics and anthropology that may prove valuable to biologists.[7]

Studies in cultural evolution have long made strong claims of analogy between cultural processes and biological evolution. It is hardly surprising that scholars have explored the possibility of a general theory of novelty and innovation spanning biological, cultural, and technological domains, although progress has been stymied by the fact that while there are many metaphorical similarities between novelty and innovation across these domains, we lack a robust theory.

Such a general theory of novelty and innovation could take several different forms:

- A general theory covering biological, cultural, and technological domains is possible, and it is possible to construct a mathematical theory through which we could evaluate the relative importance of different contributions and perhaps even make predictions about the future.

- Commonalities exist across domains, but there are sufficient differences between domains that any mathematical framework (if possible) will be domain specific.
- Commonalities exist across domains, but for various reasons developing a mathematical theory even within domains is unlikely. However, a general conceptual framework covering the three domains can be developed, while acknowledging some degree of domain specificity.
- Despite apparent metaphorical similarities across domains, processes of novelty, invention, and innovation are sufficiently specific within different domains (and may vary so much within domains) that even building a domain-specific framework is a hazardous enterprise.[8]

These alternatives will be evaluated in the final chapter.

A third major issue woven through the book is the seemingly eternal issue of continuity versus disjunction. Does novelty simply represent the extremes of adaptive evolutionary change, the sort of thing that happens every day, or are novelty and innovation somehow decoupled from evolutionary adaptation? Many evolutionary biologists reject any distinction between novelty and the sort of evolutionary adaptation that makes up much of evolutionary change, generally assuming that with sufficient time adaptive change will generate morphological novelty. Recent insights from developmental biology challenge this comfortable assumption, suggesting, for example, that the changes in developmental patterning of the embryo that led to a novelty differ from those that generate adaptive changes. Abrupt transitions, such as the appearance of turtles, seem to lend credence to claims that novel attributes and innovations represent distinct modes of evolutionary change. Defenders of more traditional approaches to evolution dispute the existence of any discontinuities, just as they have disputed the existence of distinct processes of macroevolution since the contributions of Stephen Jay Gould, Niles Eldredge, Steve Stanley, and others in the 1970s and 1980s. From this more traditional, or microevolutionary, view the seemingly abrupt shifts are a description of pattern, not of process. In the case of turtles, one could argue that poor preservation of intermediate forms generated the apparent discontinuity.

In the mid-1990s the evolutionary biologists John Maynard Smith and Eörs Szathmáry developed the idea of the major evolutionary transitions. The eight events identified by Maynard Smith and Szathmáry spanned from the origin of life to the evolution of human culture and language, thus justifying the approach taken here. They believed new evolutionary individuals were constructed during these events by changes in the organization of genetic information and in the means of inheritance, and that these transitions explained the apparent hierarchy in the organization of life. The book by Maynard Smith and Szathmáry was wonderfully stimulating and will be discussed in later chapters. But their analysis fails to adequately incorporate profound changes in the environment from oxygenation of the oceans to increases in functional complexity and the formation of new evolutionary possibilities. Indeed, this book began as a response to the major evolutionary transitions viewpoint. Among the great challenges for research on the history of life is developing an approach to this problem that recognizes the complexity of historical processes and the diversity of information required to understand them. Major transitions encompass a much more diverse array of events than those identified by Maynard Smith and Szathmáry. Their work has been properly influential in articulating a nonuniformitarian view of evolutionary dynamics: that the nature of evolution has itself changed over time.[9]

I have a broad view of the range of evolution, and I find claims of human uniqueness that justify an inviolate separation between humans and the rest of life unsupportable. Social evolution is widespread among many species, even among microbial consortia. There are aspects of human cultural evolution that appear to be unique, and certainly the extent of technology created by humans is unprecedented. But many other species modify their external environment in important ways, suggesting that the differences are of degree rather than absolute. Human evolution, particularly cultural and technological evolution, is interesting exactly because it must be encompassed by any useful approach to evolutionary innovation. And for just this reason Maynard Smith and Szathmáry included the evolution of language as the last of their major evolutionary transitions.

This issue of novelty versus adaptation and continuity and discontinuity has implications for rates of change. So far, I have said nothing about how rapidly novelties arise or how quickly novelties transform ecosystems, beyond noting lags. I would be willing to wager that not a few readers have inferred that novelties must arise quickly. Indeed, as discussed in chapters 2 and 3, many such claims have been made, but in later chapters I will argue that distinctions among adaptation, novelty, and innovation are about mechanism and are independent of the time involved. So, in contrast to the claims of my tribe (paleontologists), estimated rates may be a poor indicator of evolutionary dynamics.

Structure of the Book

Past studies of innovation, whether in biology, culture, or technology, have often relied upon compiling histories of specific cases. The case-study approach allows characteristics of novelty and innovation to emerge from the weight of examples. A more philosophical approach would be to search for definitions of novelty and innovation, emphasizing logical rigor over the messy realities of biology. Indeed, there is a growing literature among philosophers of biology and more philosophically inclined biologists proposing various definitions of novelty. Relying entirely on case studies is often justifiably criticized as anecdotal and ad hoc. The numerous informative examples in this book are in service of a broader conceptual framework. Chapters 2 through 4 examine seven different approaches to novelty and innovation, before I articulate a conceptual framework in chapter 5. Although I began this project with a rigid view of the boundaries of novelty, I have come to see that definitional flexibility is warranted. Chapters 6 through 9 employ this conceptual framework to examine different exemplars of novelty and innovation, but I will endeavor to show that these exemplars represent larger classes of similar patterns and processes.

I explore earlier approaches to novelty and innovation in chapter 2, roughly from the early nineteenth century through about 1990. I have already noted that the common assumption has been that novel morphologies are linked to the diversification of new species. I will argue that while adaptive change may often be a critical component of innovation, adaptive evolution may play less of a role than commonly assumed. Larger-scale or macroevolutionary approaches to novelty and innovation, such as the differential success of species or clades, are also discussed in this chapter. But I conclude that no model of adaptive radiation satisfactorily explains evolutionary novelty or macroevolutionary lags. Indeed, most traditional macroevolutionary approaches have neglected the factors responsible for the generation of morphological novelty.

The latter portion of chapter 2 extends the discussion of novelty and innovation to cultural evolution and technological change. Discussions of cultural and technological aspects are integrated into chapters where appropriate. But one of the challenges is the use of the term *evolution* in different fields and in different ways. Even two biologists may differ over whether the term applies to hereditary changes in gene frequencies mediated by either natural selection or genetic drift, or if selection operates at multiple levels—for example, between populations of a species. The past several decades have seen expansion of the types of inheritance to include cultural, ecological, and epigenetic inheritance. The problems increase with cultural evolution, where the focus shifts to processes distinct from the gene-centric views of many biologists. The term *evolution* becomes more confusing among economists, historians, sociologists, and other anthropologists, who may use it as a synonym for long-term change but reject any parallels with Darwinian or biological processes. While I have sought to identify similarities and differences across the domains of biology, culture, technology, and economics, I make no claim for a reductionist, gene-centric view of evolution, nor an argument for universal Darwinism. Universal Darwinism is an effort to extend a reductionist view of evolution to fields beyond biology, particularly anthropology, economics, and psychology. Instead, the focus is on the nature of novelty and innovation across domains in which the processes of change may be very different. While I use the term *evolution* throughout the book, in chapter 2 on historical approaches, chapters 3 and 9 on the domains of culture and technology, and chapter 4 on cultural spaces I use the term generically as a synonym for change, with no analogy to biological processes. Because human novelties and innovations are found today in a single species, I discuss them together in chapter 9. I make no claims for even a survey of the vast literature on novelty and innovation in economics and business.[10]

Many biologists use *novelty* and *innovation* interchangeably, and writers of popular business books rarely seem to have given any thought to the possibility of a distinction between the two terms. *Novelty* and *innovation* are what cognitive scientist Marvin Minsky termed "suitcase words": words that have a variety of meanings, like *conscience* or *complexity*. Unpacking suitcase words can transform impossible problems ("What is consciousness?") into a series of less difficult problems where progress might be achievable. Definitions of novelty, invention, and innovation differ between different authors and have changed over time. To some, novelty applies to any heritable biological change or is synonymous with adaptation, but such a definition is so broad as to be meaningless. I begin unpacking these words in chapters 3 to 5 as I examine how the concept of evolutionary novelty has been refined over the past few decades. Coincidentally, the beginnings of evo-devo, insights from the fossil record, new approaches to cultural evolution, and new tools to reconstruct evolutionary history led to reassessments of the nature of novelty and innovation, beginning about 1990. These new ideas provide the foundation for chapter 3, which advances the historical presentation over the past three decades.

I highlight how evo-devo studies have provided insights into the genetic and developmental foundations of novelty.[11]

Sewall Wright, one of the founders of the Modern Synthesis, argued that supply of genetic novelties was relatively constant through time, with their success depending on ecological opportunities. Like Mayr and Simpson he saw no useful distinction between novelty and innovation. Wright introduced the concept of an adaptive landscape as a heuristic model to depict the fitness of an organism under different gene combinations. The highs on the landscape represent regions of high fitness or adaptation, while the basins represent low fitness or adaptation. Simpson's adaptive landscapes introduced the concept of a space into evolutionary biology and became one of the most enduring and popular metaphors in evolution. Today spaces of DNA, RNA, and proteins are common, and the idea has been extended to regulatory and metabolic networks. Paleontologists analyze morphology within morphospaces, and other design spaces encompass functional, ecological, or other features of organisms. Not to be outdone, economists have described product spaces and their potential influence on economic development.[12]

We intuitively think of spaces as Euclidean, where the three axes of the space are at 90 degrees to each other and distances can be measured between objects. But many mathematical relationships between objects are not Euclidean spaces or may be only locally Euclidean. The idea of a space is a powerful metaphor that raises important questions: How accessible are different regions of an evolutionary space? Do spaces simply exist, waiting for organisms to fill them, or are they somehow constructed through the history of life? Such questions raise some interesting and poorly appreciated problems associated with the topology of evolutionary spaces, the topic of chapter 4.

Innovation is often described as a search through a space of opportunities, but this is misleading if evolutionary spaces can be constructed. I explore this fundamental difference in some detail in chapter 4 because it has some far-reaching consequences for how we think about evolutionary novelty and innovation. "Search" is the appropriate metaphor in situations where solutions are already present (what are called pre-statable spaces), and movement through the space can be accomplished via simple operations.

The sequence space of 20 nucleotides of DNA or RNA is an example I use in chapter 4. A single nucleotide mutation changes the sequence one position in the sequence space. Ignoring changes in the length of the sequence and considering just single nucleotide changes, then there are 19 possible single nucleotide changes from any starting sequence. And each of these is adjacent to additional single nucleotide changes. Thus, there is a pathway of single nucleotide changes through the sequence space from a starting sequence to a completely different 20-nucleotide sequence. A simple operation (mutations producing the substitution of one nucleotide for another) allows search through the space of alternative sequences. Some biologists argue that similar search processes explain innovation in many other systems. I will return to consider this influential example in some detail in chapter 4. In general, search operates in systems like sequence spaces for proteins and nucleotides, and even potentially for some phenotypes such as logarithmically coiled shells (clams and gastropods). But the metaphor of search becomes problematic where the design space cannot be defined independently.

My view is that most significant evolutionary novelties and innovation involve the construction of new opportunities. Construction involves the formation of a space of opportunities that could not reasonably have been specified in advance. These opportunities could be molecular, developmental, morphological, cultural, or technological, but they often involve more complicated evolutionary changes than in search. Once formed, new design spaces can be exploited by adaptive search. Arthropods, with exoskeletons and jointed appendages, represent the formation of a new space of opportunities, for example. It would have been difficult to define the possibilities for arthropods 600 million years ago, before the morphological novelties appeared. But the origin of arthropods opened a vast range of opportunities, which are continuing to be exploited.

Microbiologist Richard Lenski and his colleagues have followed the evolution of strains of the bacterium *Escherichia coli* for more than 50,000 generations. In 2011 Lenski and Zac Blount announced the discovery of a form of *E. coli* that feeds on citrate. Acquiring this capability required earlier genetic changes that created the potential for the mutation that allowed the bacteria to feed on citrate. These earlier mutations potentiated this change, but they did not themselves establish the novelty. Such potentiating mutations have been associated with other novelties as well and cast doubt on the assumptions of Wright, Mayr, and others: We cannot assume that the supply of novelty is relatively constant through time. Indeed, one of the main arguments of this book is that we need to understand the factors that control the supply of novelty and how this has changed through time. The experimental demonstration of potentiation deeply influenced the conceptual framework of novelty and innovation advanced in chapter 5.[13]

This framework involves four components: potentiation, novelty, adaptive refinement, and innovation. While ecological opportunities are important, in my view they do not play the central role in novelty and innovation proposed by Wright, Simpson, and Mayr. But by distinguishing potentiating factors and adaptive change from the generation of new morphological novelties and the environmental aspects that control whether, and when, the novelties become successful as innovations we may be able to generate a more comprehensive understanding of these aspects of evolution. The conceptual foundations of novelty and innovation are not as well developed in studies of cultural change as in biology or economics, but later chapters extend this approach to culture and technology.

The opportunity-driven view of novelty and innovation assumes that new morphologies depend upon existing genetic and developmental variation. But other evolutionary and developmental biologists have argued that novelty often requires specific genetic and developmental changes. If this latter view is correct, then the origin of novelty may in part reflect the internal dynamics of complex systems, whether they are organisms or cultures, and be largely decoupled from ongoing processes of adaptation. In my view, there is less conflict between these views than may first appear, once the nature of novelty is carefully circumscribed. Chapter 6 will consider specific cases of evolutionary novelty and the role of networks in facilitating change. The primary objective of that chapter is to address the sources of genetic and developmental novelties. The core of the chapter will involve a discussion of how the structure of developmental gene regulatory networks controls patterns of novelty.

The generation of evolutionary innovations in biological, cultural, and technological domains is addressed in chapters 7–9, including the mechanisms responsible for converting evolutionary novelties. Ecological processes are discussed in chapter 7, including those by which organisms construct niches either for their own species or for other species. In addition, that chapter considers several types of diversifications, novelty events, and innovation after mass extinctions or similar biotic crises. Chapter 8 provides case studies of biological innovation that illustrate the importance of a "macroevolutionary triad" of genetic and developmental potential, ecological opportunity, and environmental possibility.

Chapter 9 examines novelty and innovation in culture and technology. Cumulative cultural evolution, language, and cumulative technological evolution are unique human novelties that enable other novelties and innovations. Since these changes all occur among humans and our closely related ancestors, discussing these changes in a single chapter was more effective. Patterns of innovation in cultural and technological evolution exhibit many similarities to processes of biological innovation, but there are also many cases of apparently parallel innovation, as with social complexity such as states, whereas technological innovation more commonly seems to follow patterns of novelty followed by diffusion, more like some evolutionary diversifications in biology. The emphasis is on the formation of new stable structures as a key component of cultural evolution (broadly construed), focusing on macroevolutionary patterns of cultural and technological novelty, new forms of social complexity, the role of institutions, and the extent to which the model developed in chapter 5 may be applicable.

I return to the major themes discussed earlier in this chapter in the concluding chapter, emphasizing the conceptual framework developed in chapter 5, evaluating the prospects for a general theory of innovation and novelty and whether the probability of innovations has changed through the history of life, and why this might be so. One of the central themes of this book is how novelty and innovation reflect the evolution of the evolutionary process itself over the past three and a half billion years or so. The fundamentally historical nature of evolution means that the nature of variation upon which selection can act and the kinds of evolutionary changes that could occur vary across lineages and through time. New mechanisms of regulatory control create new opportunities for evolutionary novelty, while new ecological structures generate new opportunities for evolutionary innovation, just as technological inventions have expanded cultural and economic opportunities. The origin of sophisticated developmental programs in groups with complex cellular differentiation (plants, animals, and fungi) has greatly expanded the complexity of the regulatory genome relative to the possibilities in microbes. In contrast, microbes share huge libraries of genes in ways that are less common among groups with complex development. Thus, the evolutionary process has itself evolved over time, and this is just as true in the cultural domain as it is in the biological domain. I will develop the argument that the opportunity space for both novelty *and* innovation has expanded over time, a view that contrasts sharply with the idea that search through combinatoric possibilities is a sufficient explanation for innovation.

The final chapter also addresses the relationship between innovation and biodiversity. Is novelty primarily responsible for increases in biodiversity? Ecologists frequently invoke the concept of “carrying capacity,” an idea derived from population biology, that available resources are limited and constrain total diversity. While there is little doubt that the total resources available to the bacterium *E. coli* in a test tube are limited, the extension of this concept to controls on the number of species is problematic. I am interested in how novelty and innovation influence total biodiversity and changes in the structure and complexity of ecosystems. One possibility is that novelties arise continuously but succeed only if there is sufficient ecological opportunity for successful innovation. Such a situation is analogous to what economists describe as a "demand-pull" innovation, where the need for an innovation drives the process of invention. Alternatively, biological novelty could drive changes in ecological networks, constructing new niches, and thus directly influence innovation through biotically driven positive feedback. The analogue of this in economics is the creation of new markets because of technological innovation. The revolution in personal computers and related personal electronics over the past decades is an example of niche-constructing innovation.

Finally, evolution is fundamentally a deeply historical process, which raises an important philosophical issue. Is the outcome of evolution contingent upon historical events, or would similar outcomes have arisen independently of whatever historical accidents transpired? One view of evolution acknowledges the primacy of natural selection and views long-lived lineages as successful because they were better adapted than competing lineages. An argument for the importance of contingency has been advanced by Jacques Monod in his book *Chance and Necessity*, and by Stephen Jay Gould in *Wonderful Life*, among other evolutionary biologists. A different perspective has been championed by paleontologists Simon Conway Morris, George McGhee, and others. In *Wonderful Life* Gould asked: If one replayed the tape of life again would the result be similar? Is life constrained to be carbon based? To be based on DNA, perhaps even with a similar genetic code? To form animals, even arthropods or highly encephalized primates? Advocates of this alternative describe it as deterministic, because they view the evolutionary options as limited and thus likely to recur, as discussed further in chapter 4. The answers to such questions can reveal much about the opportunity space in which novelty and innovation, and evolution more broadly, operate.[14]

If evolutionary outcomes are limited rather than contingent, the details of novelty may play little role in the outcome of innovation. I will argue that although some aspects of evolution are deterministic, the historical nature of evolution generates a highly contingent dynamic for novelty and innovation. This is particularly relevant for the nature of evolutionary spaces and the distinction between novelty as search versus construction. The topology of an evolutionary space with deterministic outcomes may be very different from one with contingent outcomes. The contingent nature of novelty and innovation is further support for the argument that construction rather than search is the dominant mode of generating novelty. If this argument is correct, it has substantive implications for how we think about evolutionary change through the history of life.

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