



Review

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Author for correspondence:

Andreas Wagner

e-mail: andreas.wagner@ieu.uzh.ch

Spaces of the possible: universal Darwinism and the wall between technological and biological innovation

Andreas Wagner^{1,2,3} and William Rosen⁴

¹Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland

²The Swiss Institute of Bioinformatics, Quartier Sorge – Batiment Genopode, 1015 Lausanne, Switzerland

³The Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA

⁴147 Jefferson Road, Princeton, NJ 08540, USA

Innovations in biological evolution and in technology have many common features. Some of them involve similar processes, such as trial and error and horizontal information transfer. Others describe analogous outcomes such as multiple independent origins of similar innovations. Yet others display similar temporal patterns such as episodic bursts of change separated by periods of stasis. We review nine such commonalities, and propose that the mathematical concept of a space of innovations, discoveries or designs can help explain them. This concept can also help demolish a persistent conceptual wall between technological and biological innovation.

1. Introduction

For thousands of years, the western intellectual traditions, whether dated from the pre-Socratics or the first chapters of Genesis, have maintained a conceptual wall that separates the world of nature from that of man. However, during the past two centuries, a countervailing view has emerged. Its roots go back at least to Charles Darwin's *Origin of Species* in 1859. This Darwinian world view began to erase the distinction between human life and the rest of the natural world, and has diffused into nearly every corner of human activity. It gave rise to 'universal Darwinism', the application of Darwinian thinking to fields as different as psychology, linguistics, economics, computer science, chemistry, engineering and cosmology [1–5]. The points of contact between Darwinism and other disciplines are usually limited, often not extending beyond some form of 'selection'. However, for one distinctly human activity—technological innovation—they reflect almost everything we have learned about biological evolution in the two centuries since Darwin. Each of the next nine sections reviews a broad commonality between innovation in nature, on the one hand, and in technology and science, on the other hand. (These commonalities have been explored by many writers cited throughout, but in separate and book-length treatments, not in a concise overview.) The final section discusses the causes of these commonalities. Some of them are simple, others quite complex. Taken together, they hint at a deeper principle of *innovability* that emerges from a space of possible innovations that is independent of the history of life or technology [6]. The recognition that such a space is universally important for innovation can help erode the conceptual wall between innovations in technology and nature.

2. Trial and error within populations

Few readers will be surprised that nature innovates through trial and error, or, as it is sometimes called, trial and success [7]. Mutations that range from random changes in individual nucleotides—the four chemical 'letters' of DNA—to deletions and duplications of entire genes, and large-scale rearrangements of millions of nucleotides are inevitable by-products of imperfect DNA replication

and repair. Many such alterations change an organism's phenotype—its visible or measurable features—and produce a living experiment, a trail that can fail.

In the eyes of many, human innovation is fundamentally different. Humans have goals, whereas nature does not. Biological trials lack direction, whereas technological experimentation is highly directional, aimed at solving specific problems.

The distinction is important, but it hides a more fundamental similarity. The *process* that leads human innovators to these solutions is governed by trial and error. Even highly prolific inventors testify to its importance. Among them is Thomas Edison, perhaps the most prolific and certainly the most quotable on this subject. He tested 'no fewer than 6000 vegetable growths' as filaments for his first incandescent light bulb before he finally stumbled on bamboo as the best material—temporarily, as it would later be replaced by tungsten. He slightly exaggerated only the number of trials his inventions require when he observed, 'I have not failed. I have just found ten-thousand ways that do not work' [8]. Decades later, John Backus, one of the creators of the computer programming language Fortran echoed Edison when he said 'you need the willingness to fail all the time. You have to generate many ideas and then you have to work very hard only to discover that they don't work. And you keep doing that over and over until you find one that does work' [9].

Some trial-and-error exploration of new technology has a methodical flavour. It considers a specific problem and varies one or more parameters of candidate solutions to it. Such parametric study was central to the invention of high-speed tool steel by Frederick Winslow Taylor, who tested thousands of alloys using manganese, tungsten and chromium, at hundreds of different annealing, heating and cooling temperatures [10]. The 'father of civil engineering', John Smeaton, demonstrated the improved performance for undershot water wheels—wheels in which the water flows through the bottom of the wheel, rather than over its top—in one of the most systematic parametric experiments ever [11]. The Wright Brothers developed the wing that would be essential to the first airplanes by parametric variation of 48 different surfaces at 14 different angles in their Ohio wind tunnel [12].

Parametric testing is important, but we would be flattering ourselves if we thought this relatively rational process was the main driver behind human innovations. Multiple key innovations in the history of technology were as close to pure accidents as could be imagined. One such accident led to Thomas Newcomen's discovery of the atmospheric steam engine. It occurred when a poorly soldered seam in an engine's outer envelope broke, and accidentally injected a jet of cold water into the engine's steam cylinder, condensing the steam immediately. Because condensed steam—water—takes up less than one-tenth of 1% of the space needed by steam, this leak turned the cylinder into a vacuum chamber which exerted a huge amount of force on the engine's piston, and thus demonstrated the principle of a working steam engine [11]. Vulcanized rubber, able to retain its flexibility in a wide range of temperatures, was discovered when Charles Goodyear inadvertently dropped a compound of natural rubber, white lead and sulfur on a hot stove [13], and the world's best-known non-stick substance was discovered when a freezing experiment spontaneously turned a potential refrigerant gas into Teflon [14].

The immediate goal of an invention may be clearer to a technologist than it is to nature's blind watchmaker [15].

However, such foresight usually does not extend far, because even visionary inventors often fail to anticipate the ultimate use of their discoveries. Wireless radio was invented by Guglielmo Marconi specifically for two-way communication, and his company rejected the proposal to use the technology for broadcasting news and entertainment, even though the idea came from one of their own telegraphers, David Sarnoff, who would later found RCA [16]. Edison at first viewed his phonograph primarily as a tool for business communication [17], and while penicillin, as is well known, was accidentally discovered through a contaminated Petri dish left out on a laboratory bench by the physician Alexander Fleming in 1928, it was more than 10 years before he or anyone else realized its potential as a revolutionary medical treatment [18]. Examples such as these remind us that we overestimate our capacity for foresight.

A corollary to the importance of trial and error is that both biological and technological evolution rely not on individuals, but on populations. In biology, this was first fully realized early in the twentieth century during the birth of population genetics, the discipline that aims to describe how new variants of genes and genomes spread through populations. Although highly mathematical, some of its principles are quite intuitive: because evolution proceeds by trial and error, large populations experience more trials, and thus have a greater chance to draw the winning lottery ticket. And even though the myth of the lone inventor is firmly lodged in the public imagination, technological innovation relies on a similar principle. Edison's lighting experiments depended on a staff of dozens of assistants, so much so that one of them, Francis Jehl, said that 'Edison is in reality a collective noun' [19]. The importance of populations—from collaborating groups to competing teams—has only increased since Edison's time and is responsible for innovations as different as children's car seats and handheld computers [19].

3. Extinction and replacement

The nearly four-billion year long history of life can be viewed largely as a history of species extinction—the flip side of innovation. As many as 99.9% of all species that have emerged since life's origins are extinct today, together with the novel survival strategies they once embodied [20]. Species extinction is a constant drizzle that is sometimes punctuated by tropical downpours: mass extinctions that can kill more than half of all species in one fell swoop. And phenomenal success, over periods of hundreds of millions of years or more, offers no immunity. Sixty-five million years ago, the giant dinosaurs, along with three quarters of all other species, vanished in a geological eye blink, perhaps a few tens of thousands of years [21]. Their disappearance 65 Ma repeated the experience of most other forms that preceded them, such as the trilobites, ancient arthropods that filled the oceans until their extinction some 250 Ma.

The history of science and technology is impossibly brief compared with the four billion years of life's history, but it already has its dinosaurs, even though technological extinctions are more likely to be caused by competition rather than by huge extrinsic events such as asteroid impacts. Obsolete technologies, from the stone axe to the horse-drawn carriage and the steam engine, litter technology's battlefields. And so do outmoded scientific theories, such as Ptolemy's epicycles that allowed earth to remain at the centre of the

Solar System, or the phlogiston theory of the seventeenth century. The best explanation of phenomena such as combustion and oxidation for nearly a hundred years, it was made obsolete by the work of Antoine Lavoisier and the discovery of oxygen [22].

Extinction is not always final, as successful resurrections in nature and technology demonstrate. Aficionados of medieval coats of arms, steam engines or vacuum tube televisions have brought these technologies back to life. Thousands of enthusiasts have revived the market for old-fashioned vinyl records, whereas others delight in loading and firing black powder firearms. Such resurrection is possible only if the information needed to build an artefact or an organism is still available. From one perspective, human technology is superior to nature in this respect, thanks to humans' extensive record keeping, for example through patent applications. By contrast, records of life are written in fossils that often do not preserve much more than the shape of an organism, and certainly not the information in its DNA. Arguably, however, this comparison is not fair, given life's long history: would humans alive 100 Myr from now be able to resurrect our current technologies? What's more, resurrections of some organisms are eminently feasible, such as the recently revived bacterium *Herminimonas glaciei*, frozen 3 km below the surface of Greenland's ice sheet for 120 000 years [23]. And while the dinosaur-reconstruction fantasy of the movie Jurassic Park may remain science fiction forever, DNA molecules can already help reconstruct complex parts of our long-extinct ancestors. A case in point is the 450 Myr old ancestor of two different kinds of hormone receptors, the mineralocorticoid receptor and the glucocorticoid receptor. Computational reconstruction followed by synthesis of the ancestral protein from information in today's receptors showed that it was able to interact with both hormones, and demonstrated how subsequent changes allowed it to specialize on one of them [24]. Unlike many technologies, organisms alive today carry an extensive record of their extinct ancestry, most of it through ancient genes that continue to serve the organism, some of it through defunct genes that can persist in a genome for millions of years [25]. We have an 'inner fish' [26], but an LED has no 'inner candle'. This inner record of life may ultimately provide biologists with a great advantage in bringing back innovations from the dead.

4. Descent with modification

The best-known instance of this principle in biology is the inheritance of mutationally modified DNA from parents to offspring—'vertical' transfer across generations (as opposed to the 'horizontal' transfer discussed below). But it is not the only instance: in many animals, simple 'technologies' such as the sticks that help New Caledonian crows forage and the marine sponges that help bottlenose dolphins hunt fish are passed from generation to generation at least partly through social learning [27,28]. Such cultural inheritance is a hint that descent with modification may be just as important in the evolution of technology. And indeed it is. Archaeologists successfully use Darwinian concepts to understand the material record of prehistoric human cultures. For example, the tools of cladistics—a discipline that reconstructs evolutionary history from patterns of inheritance with modification—have been used to construct a phylogeny of the many forms of fluted points used in projectile weapons, such as arrowheads and spear points, of

Palaeo-Indian cultures [29]. A recent study of more than 100 separate design traits found in Polynesian canoes, including the shape of the outrigger boom, the fibres used for lashing attachments together, as well as the length and depth of the keel and ribs, identified a clear pattern of descent by modification [30]. The table fork first appeared in Europe in the early fourteenth century in a two-tined version, was slowly supplanted by one with three tines, and then, in the seventeenth century, by a four-tined fork, which has not changed substantially since [31]. And twentieth century innovation is also essentially a litany of descent with modification. Examples include cars (Ford's Model T to the Prius), planes (the Wright's Brother's Flyer to the Boeing 787) and programming languages such as Fortran, which radiated into multiple different successor languages, such as ALGOL, BASIC and Python [32].

5. Horizontal information transfer

The cornet is a nineteenth century brass wind instrument that uses valves to produce different notes by changing the shape of a vibrating chamber. Its history illustrates that descent with modification is augmented by a form of horizontal transfer between contemporaneous innovators. The reason is that two different valve systems—the Stölzel and Périnet systems—were developed over time via such information transfer. When one designer shifted valve location and alignment, or the placement and shape of the bell, the other recognized the innovation, and incorporated it. The Stölzel valve, one hollow cylinder inside another, appeared first, in 1825. It controlled airflow by admitting the air along its longitudinal axis. About 1840, the Périnet valve 'solved' the same problem by controlling the airflow across its width. The Périnet valve did not just derive from its 'ancestor', but was a solution that also depended on horizontal information transfer [33,34].

At least since the invention of written information transmission, knowledge has been travelling between individuals and groups at an accelerating pace, thus facilitating such transfer. Examples old and new abound, from gunpowder, which was invented in China in the ninth century and spread from there [35], to horses, which were introduced to the New World by the Spanish conquistadores and eventually helped turn North American Indians into the fearsome warriors that held expanding European settlements in check for decades [36]. They also include post-industrial technologies such as—once again—programming languages, in whose radiation horizontal transfer of language elements play a role, such as in the creation of BASIC, which combined elements of Fortran and ALGOL [32].

Horizontal transfer is not a feature that that sets technological innovation apart from nature's innovation. To argue otherwise is to ignore a key mode of innovation in the most populous and prolific organisms on the planet: bacteria. The information they exchange comes in the form of genes, which can get transferred through viruses, through a cell's uptake of naked nucleic acids from the environment, or through a primitive form of sex called bacterial conjugation [37,38]. Such horizontal gene transfer can alter genomes on short evolutionary timescales [39–44]. For example, it adds DNA to the *Escherichia coli* genome at a rate of more than 60 genes per million years [45,46]. Even closely related strains of a bacterium like *E. coli* can differ in more than 20% of their genome, and may have more than 100 added genes relative to

other strains [43,44]. Horizontal gene transfer is so prevalent in bacteria that their evolutionary relationships may not resemble so much a tree as a network, where the lineage of any one species is a mosaic of different genetic influences [47]. And most importantly, horizontal gene transfer is responsible for a wide variety of bacterial innovations, such as the ability to digest and degrade toxic molecules, the ability to cause infectious diseases, as well as the rapid spreading of antibiotic resistance through worldwide bacterial populations [37]. While rampant in bacteria, such transfer has also been observed in other organisms, such as between yeast and fruit flies [48]. In general, however, horizontal transfer becomes rarer in distantly related organisms [49,50], which provides another parallel to technological change, where the diffusion of innovations and ideas was historically far more frequent *within* societies, and especially within those that share a scholarly tongue—medieval Europe, or Islam, or China—than between them [51].

The boundaries between descent by modification and horizontal transfer are not clear cut, which is obvious in technological change, but just as true in biology. The best illustration is sexual reproduction in organisms such as us. It involves a form of horizontal transfer that shuffles genetic information between two organisms in the same population, but this shuffling always leads to reproduction—vertical descent. This stands in contrast to bacterial sex, where horizontal exchange is independent from vertical information transmission. The power of mixing vertical descent with horizontal exchange is best illustrated by its prevalence in higher organisms. With few exceptions, lineages without the ability to reproduce sexually are evolutionary dead ends. Most of them have only emerged recently in evolution and do not persist for long. Creating new variation is one of several reasons for the prevalence of sex ([52], ch. 15).

6. Combinatorial innovation

The importance of horizontal gene transfer foreshadows our next principle, namely that innovation frequently results from assembling what already exists into new combinations—recombination, in the most general sense of the word.

Consider pentachlorophenol, a highly toxic man-made molecule introduced in the early twentieth century, used as an insecticide, fungicide and disinfectant. Some organisms, such as the aptly named bacterium *Sphingobium chlorophenolicum* thrive on it, using pentachlorophenol as their only source of energy and carbon. This bacterium converts pentachlorophenol into a less toxic molecule that it can feed on, with the aid of four chemical reactions that are catalysed by enzymes and encoded by genes. Individually, these reactions occur in many other organisms, where they help recycle superfluous amino acids in some, and disarm various toxic molecules in others. The innovation of *S. chlorophenolicum*—brought about by horizontal gene transfer—lies in the new *combination* of these enzyme-catalysed reactions. Similar recombination also occurs in other metabolic innovations, such as the urea cycle of land-living organisms, a once-novel cycle of five enzyme-catalysed chemical reactions that helps them detoxify ammonium waste and excrete it in their urine as urea. The individual reactions are widespread in other organisms, and help manufacture or recycle amino acids. What is novel is their combination [53].

Perhaps the clearest illustration that innovation in nature is combinatorial comes from the biological macromolecules

ribonucleic acid (RNA) and proteins. Each of these polymers is a string of simpler building blocks—four different nucleotides in the case of RNA, and 20 amino acids in proteins—that play thousands of different roles in the life of any organism, from regulation to transport, communication and catalysis. All of these functions arose by changing the individual nucleotide sequence of an RNA or protein molecule. Put differently, new molecules of this kind are simply new combinations of a few chemical ‘letters’.

The most familiar analogy to this process is cultural: the same 26 letters, plus a few punctuation marks, can be reshuffled to produce *Great Expectations* or *The Great Gatsby*. However, technological innovation is also combinatorial in less obvious ways. A typical and much cited example is the jet engine that transformed aviation in the middle of the past century [54]. It consists of three components: a compressor, a combustion chamber and a rotating turbine. Each of them has a long history of functions unrelated to generating thrust. Compressors, in the form of bellows, had been a core technology for blacksmiths for more than 2000 years. Combustion chambers are essential for the internal combustion engines of automobiles. And the precursors of screw turbines have existed since Archimedes. The power of combinatorial innovation is just as apparent in less complex technological innovations. The bench vice, for example, is a powerful eighteenth century combination of two simple machines that date to antiquity, a lever and a screw. The front-mounted wheelbarrow, which first appeared in Europe in the twelfth century, combines the mechanism of a lever with that of a wheel [55]. Newer but just as useful is the adjustable wrench, which combines the mechanical advantage of a lever with that of a screw.

The insight that combinatorial innovation pervades technology just as it pervades nature is not recent. When the economist Brian Arthur [54] states that ‘technologies somehow must come into being as fresh combinations of what already exists’ he is extending the ideas of the economist Joseph Schumpeter [56], who defined entrepreneurship as the creative recombination of existing ideas. Another economist, Joel Mokyr [57], has argued that a new technological process—a ‘technique’ in his formulation—appears when the knowledge underlying two different techniques is joined in a novel fashion.

7. Exaptation

The ubiquity of combinatorial innovation has a corollary. In an innovation, the parts of a biological or technological system are often co-opted for new purposes unrelated to the reasons for their origin. In biology, this phenomenon was known to Charles Darwin more than a hundred years before the late palaeontologist Gould [58] christened it *exaptation*. Darwin [59] reminded readers of the *Origin of species* that ‘an organ originally constructed for one purpose . . . may be converted into one for a widely different purpose . . .’ (p. 175), using examples such as the transformation of flotation bladders of fishes into the lungs of terrestrial animals. Thousands of others examples known today include the feathers of birds, which originated most likely to insulate or waterproof a body, and were only later ‘exapted’ for flying [60]. Made especially famous by an eponymous essay of Gould [61] is the Panda’s ‘thumb’, an extra digit that helps this herbivore strip leaves from bamboo stalks, the better to eat only the shoots. Because the Panda’s forearms also have five regular

digits, this thumb cannot share a common ancestry with our thumb. It happens to be a greatly enlarged wrist bone, equipped with muscles and co-opted for a new use.

Exaptations permeate life down to the level of molecules. One exapted molecule is lysozyme, an enzyme that helps organisms defend themselves against bacteria by killing them. This enzyme has been co-opted in mammals to help them synthesize lactose, a prominent sugar in mammalian milk [62]. Another example is a protein called 'sonic hedgehog', which helps sculpt fingers and the spinal cord in our bodies, but moulds feathers in birds [62]. Such molecular exaptations illustrate that some innovations can originate as mere by-products of evolution, for no adaptive reason at all. Examples include hundreds of promiscuous enzymes, so-called because they catalyse a main chemical reaction that is important to an organism's survival or reproduction, but also a spectrum of side reactions that can later become adaptations [63–65]. At least as abundant are insertions of transposable elements—mobile pieces of DNA that can change location within a genome—near a gene. They often happen to carry stretches of DNA that can activate the nearby gene, which is often inconsequential at first but can come to provide a benefit later [66].

Exaptation is no less ubiquitous in technology than in nature. A classic example is Johannes Gutenberg's printing press, which, in the words of Stephen Johnson 'borrowed a machine designed to get people drunk'—a screw-driven wine press—and turned it into an engine of mass communication' [67]. Microwave ovens heat food with a technology originally developed for radar—the first commercial version was called the 'Radarange' [68]. The powerful and quick-acting cyanoacrylate adhesive marketed as 'loctite' 'super glue' and 'krazy glue' was discovered by researchers at Eastman Kodak working on plastic gun sights for World War II combat aircraft [69]. Once one accepts the combinatorial nature of both kinds of innovation, the importance of exaptation in both nature and technology comes as little surprise.

8. Ecosystem engineering

A beaver that builds a dam and a lodge creates not only shelter from wolves and other predators through impenetrable mud walls, easy access to food through underwater entrances, and a dry den to raise its family, but it also engineers an entire ecosystem. Beaver dams restore wetlands that can house many species, such as salmon and frogs, provide flood control and nourish bacteria that feed on decaying cellulose and absorb excess nutrients such as phosphates and nitrates.

Organisms that engineer ecosystems, a process also known as niche construction, transform their environment, whether actively like the beaver or passively through their mere presence. And such organisms are legion. They include the more than 10 000 species of nest-building ants and termites. They also include the trees in terrestrial forests, which change the cycling of water and thus affect the weather experienced by all organisms around them. And they include microbes such as oral bacteria that secrete sticky polymers to form biofilms that protect them from the assault of toothbrushes, and marine phytoplankton that can increase ocean surface temperatures through light absorption and scattering [70,71].

The most important point about ecosystem engineering is not that it creates new environments, but that these environments can guide future innovations.

Some frogs and reptiles that construct their niches through burrowing have evolved specialized limbs and hardened snouts to help them do so. Ants not only build nests, they also have evolved the ability to regulate a nest's temperature by plugging holes to prevent heat loss, or by adjusting a mound's slope to change heat absorption from the Sun. Some burrowing spiders can equip their surroundings with silken trip wires to alert them to a prey's approach. Weaverbirds first evolved the ability to build simple nests, and only later the skill to elaborate these structures, such as by building roofs to keep their chicks dry.

Radically new kinds of niches—their origins go back to life's earliest times—even create platforms for change that can give rise to entirely new forms of life. The evolution of photosynthesis transformed our atmosphere from a mix of toxic gases to its present oxygen-filled state, which made the life of animals and humans possible in the first place.

A bit later, the conquest of land by animals created a new platform—literally—for terrestrial life, on which organisms as diverse as dinosaurs, birds and mammals arose.

The technological innovations of humans also transform the environment, with numerous parallels to ecosystem engineering in nature. For example, Jones *et al.* [71] write in a review on ecosystems engineering that 'from a functional perspective we see no difference between human and non-human engineering' (p. 379). And like in nature, new technologies create new niches [72], platforms for future innovations. This has been the case throughout the history of technological evolution, whose key moments Schot & Geels [73] define as 'the establishment of a new sociotechnical regime', that is, any change that transforms the way people interact with technology.

Examples include the wheeled mouldboard plough, which first appeared in Europe during the Middle Ages, allowed the cultivation of heavy soils, and thus enabled the production of enough cereal grains to feed the continent's growing population [74]. That increased population, in turn, required the deforestation of millions of acres to produce more arable land, an activity that demanded innovations in the blast furnaces and forges that manufactured iron axes for an entire continent [75]. More iron meant fewer trees, until the eighteenth century, when the scarcity of charcoal fostered yet another innovation, the use of the purified charcoal known as coke. This is the fuel that not only smelted the iron for the Industrial Revolution's locomotives, but also ran them [76].

As on land, so at sea. In the tenth century, Viking long ships connected the Old World and the New World for the first time, using the technological innovation known as a sun-compass, a circular sundial with an adjustable gnomon whose shadow would hit a particular spot on the circle at noon, indicating the ship's latitude, and so allowing dead reckoning [77]. As the technology of sailing improved, the range of potential trading and raiding expeditions improved with them, demanding still more technological improvements, as the sun-compass gave way to the mariner's astrolabe, followed successively by the backstaff, the octant and the sextant, each one an innovation in navigation required for voyaging further and further from land [78].

9. Episodic change

In addition to the commonalities that we have already encountered, biological and technological innovations also share a similar rhythm. In both spheres, the rate at which innovations appear is not smooth and regular, but sharply episodic.

Ever since Darwin himself, biologists have been puzzled by the scarcity of fossils that document transitions to major innovations, despite exceptions such as *Archeopteryx*, which marks a transition between dinosaurs and birds, *Tiktaalik*, a more than 350 Myr old four-limbed fish [79], or *Runcaria*, a precursor of a seed-bearing plants [80]. The rarity of such transition fossils cannot always be explained away by an incomplete fossil record, as generations of palaeontologists chipping away at nature's secrets have learned. Nature's motto seems to be 'hurry up and wait'. In many lineages, little change is happening most of the time and when change happens, it happens rapidly. Such stasis, interrupted by rapid, punctuated change is well documented in some bryozoans ('moss animals'), small plant-like marine animals that form colonies by budding-off small 'zooids'. Some fossil American bryozoans persist virtually unchanged for up to 16 Myr, only to give abruptly rise to new species in a blink of the geological eye [81,82]. In some trilobites, eye architecture remains unchanged for long time intervals, only to change abruptly after such a period of stasis ([83] ch. 6). The most dramatic example of such punctuated change is the Cambrian explosion itself, a short period of geological time more than 500 Ma that brought forth all major animal groups alive today ([83] ch. 7).

The history of technological evolution displays a very similar pattern of episodic change, with long periods of relative stagnation punctuated by periods of major change such as the Industrial Revolution. Such bursts of innovation are often characterized by singular 'macroinventions', dramatic leaps of innovation such as the first atmospheric steam engine that are by definition rare. Perhaps the most significant example of technological stability punctuated by episodic change is the technology of information transfer. Kilgour, in *The Evolution of the Book*, cites only four significant innovations in the entire history of written communication: The clay tablet of 2500 BCE, the papyrus roll/scroll of 2000 BCE, and the codex (i.e. the modern leaved book) around 150 CE, which has been virtually unchanged until the advent of the e-book around 2000 BCE [84].

Macroinventions are to technology what the evolutionary leaps that the twentieth century geneticist Richard Goldschmidt called 'hopeful monsters'—dramatically changed organisms that are not necessarily improvements—are to biology [85,86]. There is no gradual movement from semaphore to electrical telegraph, or from telegraph to the first radio transmission by Marconi, or from transmissions that used relatively long electromagnetic waves (more than 1000 m) to shortwave (less than 200 m) transmissions [51]. Such macroinventions are complemented by microinventions, incremental improvements in existing technologies analogous to the gradual adaptation typical of biological evolution, which can either precipitate or follow macroinventions. The slow accumulation of small technological changes can cause a tipping point towards a giant improvement, such as in the e-book reader, the most recent macroinvention of reading technology. It was facilitated by dozens of microinventions, from the development of hypertext at Stanford

Research Institute in the 1960s [87] to electronic paper displays, invented at MIT in the 1990s [88]. Conversely, macroinventions can also enable microinventions. In Kilgour's example, the printed codex was successively improved by printing with movable type by Gutenberg in 1450, by steam power in the nineteenth century, and by offset printing in 1970 [84].

10. Multiples and singletons

Breakthroughs in science and technology may be rare, but history documents numerous occasions in which they appeared more than once, and independently from each other.

Already in the 1920s, Ogburn & Thomas [89] compiled more than 100 cases of independent discovery and invention. The sociologist Merton [90,91] built on their work in the 1960s and called such discoveries 'multiples'. Notable examples in science include the virtually simultaneous formulation of calculus by Newton and Leibniz, and of logarithms by Joost Bürgi and John Napier. The physical law that holds a gas's pressure inversely proportional to its volume is known as Boyle's Law in most of the world, but as Mariotte's Law in Francophone countries, respectively, for Robert Boyle and Edme Mariotte, who discovered it independently. The father of the Hungarian mathematician János Bolyai, who formulated non-Euclidean geometry at the same time as the Russian Nikolai Lobachevsky, observed, 'mathematical discoveries, like springtime violets in the woods, have their season which no human can hasten or retard' (cited in [92]). Even the theory of evolution by natural selection was famously formulated simultaneously and independently by both Darwin and Alfred Russel Wallace. And likewise for new technologies. The world's first practical steamboats were independently invented by the Americans Robert Fulton and James Rumsey and the Marquis de Jouffroy, a French aristocrat [11]. Elisha Gray and Alexander Graham Bell filed for a patent on a working telephone on the same day in 1876 [89]. Patents for incandescent light bulbs were granted more than 20 different times before Edison [32].

Multiple origins also abound in biological innovation, although not necessarily with near-simultaneity. Perhaps the best-known examples of such *convergent* traits are lens-equipped eyes in vertebrates and in the octopus, as well as the wings of insects and birds. They have plenty of company. In a 2006 paper, the palaeontologist Geerat Vermeij listed more than 50 innovations with independent origins, as different as the leaves of plants, which originated both in land plants and in aquatic plants such as algae, the production of silk in spiders and silk moths, and the electrosensory organs of African and South American fish [93]. And once again, convergent origins occur on all levels of the biological hierarchy, down to the molecular level. Take the innovation that solved a crucial problem of early life, how to extract carbon—a key building material for cells and organisms—from carbon dioxide in the air. The best-known solution is that of plants, which use the energy of sunlight and an enzyme called ribulose-1,5-bisphosphate carboxylase oxygenase (rubisco) to attach carbon dioxide to a sugar which is then incorporated into biomass. However, this solution is not the only one. Some microbes attach carbon dioxide to the carrier molecule acetyl-CoA, yet others add it to molecules from the ancient citric acid cycle [94].

Molecular examples such as this one also show that independently discovered solutions are often different from one another. Organisms can detect light waves using either a flexible single lens such as ours, or the rigid compound eye of a fly. Crystallins, the transparent proteins in eye lenses that help us, other vertebrates and molluscs create sharp images on the retina originated from enzymes, but from enzymes with different function and structure [95–97]. And antifreeze proteins have originated independently in Arctic and Antarctic fish from ancestral proteins with different functions [95,96].

Other innovations are what Merton called singletons [98], which occur either because a problem has only a single solution, or as the result of what the biologist Francis Crick termed a ‘frozen accident’ [99]: one among multiple potential solutions that happened to be discovered first, and prevents the adoption of later and perhaps superior solutions through the self-explanatory *first mover advantage* [100]. Aside from the most familiar QWERTY keyboard, which is not demonstrably superior to other layouts [101,102], the ‘Audion’ vacuum tube patented by Lee de Forest in 1908 also falls into this category. It became the standard for early radio, though technologies based on the oscillating arc or the frequency alternator could have served just as well [57]. In a similar vein, the world’s standard railway gauge, used today on more than 60% of all railroads and virtually all high-speed lines—4 feet, 8.5 inches—is the same as the one used for the horse-drawn rails at Killingworth Colliery in 1814, when the engineer George Stephenson used them for his experimental locomotive [11,103].

We cannot be certain whether singletons in biology are truly frozen accidents or superior choices [93], but some candidates for frozen accidents do exist. Most biological processes use only one of two or more mirror-symmetric, but otherwise completely equivalent, forms of the same molecule [104]. Our bodies use adenosine triphosphate (ATP) as a universal energy currency, though related molecules such as guanosine triphosphate could do the same job. Another candidate for a frozen accident is the inverted organization of our retina, which is demonstrably *inferior* to alternatives such as that of the squid’s eye: our light-sensing cells are removed from the light-exposed surface by layers of blood vessels and nerve cells, whereas these cells are on top in the squid’s retina, closest to the light [105].

11. Spaces of the possible

Most commonalities between innovation in nature and technology need little explanation. Trial and error in populations become self-evident necessities, once we accept that humans—like nature—are very poor at anticipating successful innovations. Similarly, extinction results inevitably from limited space and resources in both the natural and technological world. Vertical and horizontal transfer of information are the only two principal modes by which one could tinker with the old in order to create the new [106]. And such tinkering is inevitable in a non-creationist world, where the new does not emerge in perfection.

The reasons behind other commonalities are less obvious, but in biology, a framework has emerged that can help explain them, and that is relevant for technological innovation. We will illustrate it with proteins, a specific class of systems involved in many innovations, but it applies also to

all other systems known to be involved in molecular and macroscopic biological innovations [6].

At each position of the amino acid string that constitutes a protein, one of 20 different kinds of amino acids can appear. There are $20^{100} \approx 10^{130}$ such strings for proteins that are 100 amino acids long. Fewer than 20 kinds of amino acids may suffice to create proteins with most functions [107], but because proteins can be thousands of amino acids long, it is safe to say that the space of possible proteins—of amino acid sequences or protein *genotypes* [108]—is enormous. Inside an organism, most proteins fold in three dimensions through thermal motion, and this *fold*, which constantly wiggles and vibrates, is responsible for what a protein can do, its *phenotype* and function [109]. Because protein genotype space comprises all possible proteins, it also comprises proteins with all possible functions, and thus all possible innovations that involve proteins.

The very existence of such a space already helps explain the combinatorial nature of innovation and the ubiquity of exaptation. Both emerge very naturally from the realization that new proteins are new combinations of old amino acids, and such combinations almost inevitably provide new uses for the old, and thus create the potential for exaptation. What is more, because the framework of genotype space applies to innovations beyond new proteins—involving novel forms of regulation or of metabolisms—it can help explain the combinatorial nature of all biological innovation [6].

To understand Merton’s multiples in biology, one needs to go beyond the mere existence of genotypes spaces and understand their internal organization. This organization is highly peculiar, and shared among different kinds of genotype spaces [6]. Specifically, any one phenotype is usually formed by astronomically many different genotypes. For example, there are myriad different amino acid strings that have the same fold and function. What is more, many of these genotypes form connected networks [6,110]. In such a *genotype network*, the smallest possible change in a genotype—the alteration of a single amino acid in a protein, for example—can lead to a ‘neighbouring’ protein with the same phenotype. A series of further such changes can transform the starting genotype, and create an amino acid string with little resemblance to that of the starting protein, but—and this is important—through all this genotypic change, the phenotype can remain unchanged. Biological examples of Merton’s multiples are a consequence of this organization. All the genotypes in a genotype network can be viewed as different solutions to a given problem, such as how to catalyse a particular chemical reaction. Through the haphazard way in which biological evolution explores genotype space, it is apt to discover different solutions in different organisms, merely because so many different solutions exist. (These networks have a straightforward relationship to fitness landscapes [111], a concept central to evolutionary biology where genotypes are assigned different altitudes in a multidimensional landscape according to their fitness: genotype networks correspond to contour lines in such a landscape, formed by genotypes with approximately equal fitness.)

Some innovations may be only a few mutations away from an already existing genotype, but others may reside very far away in genotype space. To find them, many trials (and errors) may be necessary. What is more, improving existing innovations can become more and more difficult as these innovations approach perfection in any one

environment. Sometimes, further improvement is impossible unless the environment itself changes and triggers opportunities for more innovation. Episodic evolution, where bursts of innovation inevitably alternate with periods of stasis is, like the ubiquity of multiples, a natural consequence of the vast size and organization of genotype space [112,113].

Technological systems share the very properties—multiples, combinatorial innovation, etc.—that genotype spaces can explain in biology. This suggests that explaining these commonalities requires analogues to genotype spaces in technology. Such an analogue would harbour all possible solutions to problems that can be tackled with a given technology. One might call it a discovery or innovation space—it has also been called a design space [114]—because it contains all possible innovations that a technology allows. Like the genotype space of proteins, it is a space of the possible.

The idea that technological innovation takes place in such a space is not a mainstream notion, but neither is it new. It goes back at least to the ‘mechanical alphabet’ of machines proposed by the eighteenth century Swedish industrialist and inventor Christopher Polhem [115]. The letters in this alphabet are simple machine parts, including wedges, screws, levers and winches. Polhem believed that one could build any mechanical device by combining these parts. In a similar vein, the art historian George Hersey and computer specialist Richard Freedman searched for a way to characterize the essence of buildings designed by the famed sixteenth century Venetian architect Andrea Palladio [116] and formulated a computer algorithm that can generate thousands of different floor plans—all recognizably Palladian—based only on a small number of simple rules that subdivide a rectangular building into smaller rooms. More recently, Sanchez & Mahoney [117] have pointed out that the automobile, aircraft, consumer electronics and other industries build many different products by combining a limited number of ‘modular’ components.

All human innovation takes place in some space of the possible, but human innovators do not yet take advantage of this space in the way evolution does. For example, combining a compressor, a combustion chamber and a turbine into a jet engine [54] is dependent on ingenuity—it is not obvious how to combine the elements of an existing technology to innovate. The blind innovation process of nature compensates for its lack of ingenuity by using components whose links are standardized, such that their combination does not require ingenuity, but only patience. A case in point is the peptide bond of proteins, a type of chemical bond that allows any two of the 20 proteinaceous amino acids to connect to one another. It is this peptide bond that allows nature to explore myriad different amino acid sequences. Other examples of standardized linkages include that between regulatory proteins and the DNA sequences they bind, which help build and alter gene regulation patterns, and, most fundamentally, DNA itself, whose nucleotides are linked through the standardized phosphodiester bond, which allows mindless exploration of myriad possible DNA strings, no ingenuity required.

Standardized linkage makes a systematic exploration of an innovation space possible. And while we know about it mostly from nature, it is not beyond human technology, as the example of digital logic circuits—the heart of digital computers—shows. Their power lies in the wiring. In any one such circuit many logic gates, elementary units capable of simple

computation are wired together, and their specific wiring pattern allows them to perform the complex computations that run devices from simple calculators to smartphones to desktop computers to data warehouses and servers that maintain the entire Internet [118]. Different wiring patterns of few gates can create an enormously diverse family of circuits, and, in some circuits, this wiring can be changed while a circuit is operating [118].

Logic gates are analogous to amino acids, their (standardized) wiring is analogous to the peptide bond, and the computation that this wiring allows is analogous to the fold and function of a protein. Recent work has shown that a circuit space defined by all possible wirings of a few logic gates, has an organization similar to those of protein space [119]. And exploring this space in the trial-and-error way of biology would reveal properties such as Merton’s multiples—circuits with different wiring but the same function.

In sum, the organization of innovation spaces in biology can help us understand some of the more mystifying commonalities between technology and biology. (If innovators have not traditionally thought about innovation in these terms, it is because the organization of an innovation space is not as clear-cut in most technologies as in the digital circuit example.) And this organization may even help accelerate future innovation. Evolutionary principles already do, in the field of evolutionary computation, which develops powerful techniques that mimic evolution by mutation and selection, and that can reproduce known innovations and create new ones, for example in electronics [120,121]. However, technologists could take even better advantage of nature’s innovability, at least for technologies whose innovation spaces are like those of nature. These will be technologies where few kinds of parts are connected in standardized ways, and where multiple configurations of these parts can solve the same problems.

The points of correspondence between biology and technology we discussed are far from complete [32,67,122]. However, they already insinuate that highly successful biological and technological systems share a property that is independent of both biology and technology. This property, one might call it *innovability*, emerges from the organization of a space of possible innovations, designs or genotypes [6]. Because such spaces are mathematical concepts, one could easily dismiss them and their organization as figments of our imagination, were it not for what Nobel laureate Eugene Wigner called the ‘unreasonable effectiveness of mathematics’ in explaining the natural world [123]. It suggests that such spaces and the innovations therein have an existence beyond our limited minds. And while concepts such as this, for more than two millennia, were the subject of non-experimental disciplines such as mathematics and philosophy, they have now become accessible to experimental science. For example, recent technological advances in biology permit the synthesis of arbitrary new protein genotypes. In doing so, they also permit the exploration of a genotypes space through experiment and computation [124–126]. Technological systems are not far behind, as explorations of digital circuit spaces testify [119,127]. Efforts such as this will undoubtedly accelerate the demolition of the conceptual wall separating biological and technological innovation.

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