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Multiple Orders in Biology

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1. Ways of finding order in biology

On the face of it, the world of living organisms exhibits some striking differences from the non-living realm. Living organisms stand in a non-equilibrium relation with their environment and must extract energy and matter from their environments to build and repair themselves. Growth and reproduction are further hallmarks of most forms of life. Moreover, organisms regularly extract information about their internal constitution and external environment and alter their internal processes, external activities, and even their genetic constitution in response. While these and a few other generalities apply across living forms, the specifics about how living organisms accomplish these things are highly varied. There are an enormous number of life forms, employing a myriad of mechanisms to maintain themselves and leave descendants. Overall, the biological world appears far from tidy but rather highly disordered.

Such variability in the natural world would seem to be an impediment to modern science, which has tended to emphasize the discovery of general laws. Following the successes of Newton, who advanced a few general laws that explained a wide range of phenomena, many philosophers saw physics as the model of scientific explanation to which all other inquiries should conform. Yet biology has been stubbornly recalcitrant to such approaches, leaving many to think that biological phenomena are of a qualitatively different sort from those studied in physics. Immanuel Kant famously asserted that there could never be a Newton of a blade of grass. His skepticism for the prospects of a scientific biology arose from the fact that organisms display characteristics that machines never could, such as interdependence and self-generation.

Kant's favored solution was to recognize teleology – an irreducible goal-directedness or purposefulness – in all biological systems. Teleological explanations have enjoyed only marginal scientific status following the introduction of evolutionary theory, but the question of biological order in the scope of the natural world has continued to exercise many thinkers. Biologists have developed several strategies for finding order amongst living organisms, of which we will focus on three—taxonomies; mechanistic explanations; and evolutionary patterns of descent with modification. We will argue that these strategies have provided important organizing principles for biologists. We will also show, however, that even as these tools bring some order to biology they also give rise to complexities that frustrate any hope of some manageably simple mode of order. Thus, biology manifests multiple taxonomic schemes that serve different scientific objectives, mechanisms organized in ways that generate complex behavior, and descent relations that involve horizontal as well as vertical exchanges of

genetic material. While seeking order, biologists have to adapt their aspirations to the phenomena they seek to understand.

2. Sorting things out

One way biologists generate order in nature is by developing classification systems. By placing things in categories, we acquire ways to name and make generalizations about them. We can make certain inferences based on knowing that some creature is a vertebrate, and even more specific inferences if we know its exact species. Most biological classification is hierarchical, sorting groups and sub-groups into ever smaller and more specific categories.

Classification might seem like an uncontentious activity, something akin to stamp collecting, which has scientists unanimously agreeing to place particular objects within their most natural groupings. A close examination of scientific practice, though, reveals that such groupings are neither undisputed nor particularly natural. This is true not only in new biosciences, but even in the most traditional areas of science, like astronomy. After being classified as a planet since its discovery in 1930, astronomers in 2006 demoted Pluto to the new category of dwarf-planet, because of updated ideas about what it means to be a planet. (One of the scientists responsible for the re-organization wrote a book called *How I Killed Pluto*.) Biologists have dealt with such taxonomic debates for a very long time.

The 18th century Swedish naturalist Linnaeus inherited from the ancient Greeks the belief that behind the variable appearances of organisms are essences in virtue of which an organism is what it is. Linnaeus developed a classification scheme that arranged organisms into kingdoms, orders, families, genera, and species based on objective similarities in these essences. The essence shared by members of a species provided necessary and sufficient conditions for an individual to be a particular species. The thought here, as with other putative natural kinds such as the periodic elements, is that some particular essence – a unique trait - will be found that can identify an organism as a member of a kind, providing an objective ordering principle for the classification.

Species remains the foundational unit of classification but, following Darwin, they are also the unit of evolution: it is species that evolve, not individuals or higher taxa. But this second role for species has posed a challenge to the essentialism underlying Linnaean classification since crucial to evolution is the idea that species can evolve into other species and that in the process any traits they possess can vary. On the most common criterion, once organisms differ from one another sufficiently that interbreeding is not possible then a species has split into two. Given the range of traits on which differences can prevent interbreeding, this perspective undercuts the assumption that there are necessary and sufficient traits defining species. It also

explains why it has been so notoriously difficult to identify such traits and why the boundaries between species are often vague. The challenge to find order is further complicated by the fact that biologists appeal to multiple species concepts, including not just versions that focus on reproductive compatibility, but ones which emphasize shared evolutionary lineage and shared use of an ecological niche.

These different ways of organizing open the door for disputes between biologists about how order is best achieved. An extremely heated controversy emerged among systematists in the mid-20th century about how to organize categories above the species level. Influenced in part by positivism in philosophy, taxonomists known as *pheneticists* sought objective measures of similarity between species, especially with respect to morphological traits, while avoiding any speculative or theoretical considerations such as evolutionary descent. They produced dendrograms (Figure 1, left) designed to represent overall similarity: the shorter the lines from the branch point between two species, the more similar they are. These pheneticists were challenged by cladists (also known as *phylogenetic taxonomists*) who made descent relations primary in classifying organisms. They produced cladograms (Figure 1, right) in which the branching structure represents speciation events. Species fall within taxa that group together ancestral species and all their descendants, irrespective of their similarity. While cladists were generally viewed as the victors in this controversy, the field remains highly contentious as variants of each approach are developed. While taxonomies offer ways to order species, there is far from a consensus as to what this order will be like.

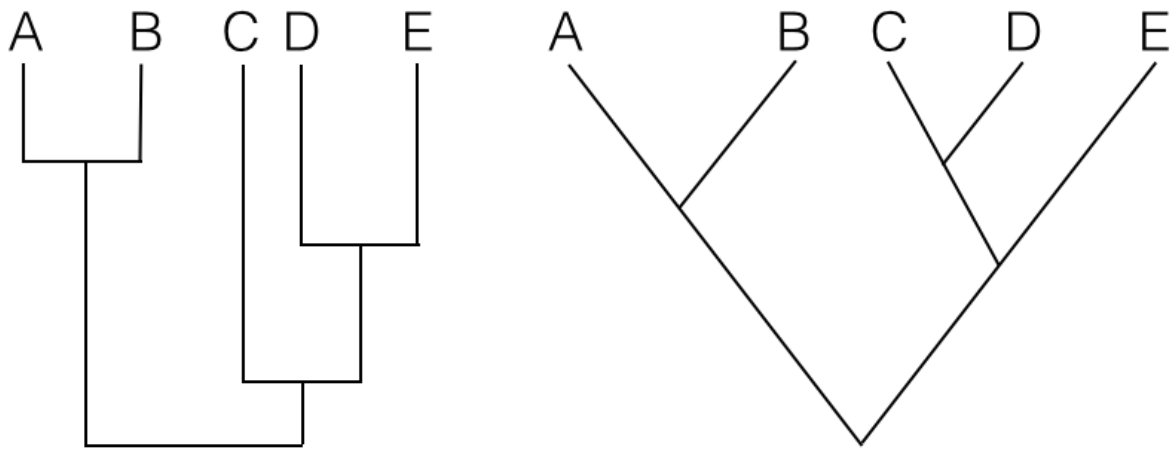


Figure 1. Dendrogram as used in numeric approaches to taxonomy and cladogram as used in cladistics approaches.

Classification is not just controversial in the case of species. We briefly discuss two other examples where biologists have tried to establish order—among proteins and

psychiatric disorders. Proteins are extremely important molecules in living systems since they enable most chemical reactions. Initially they could only be identified in terms of the reactions they enabled, but by the middle of the 20th century investigators established that proteins were composed of amino acids bound sequentially into polypeptide chains, and began to identify the distinctive sequences of different proteins. The *Atlas of Protein Sequence and Structure* advanced a categorization of proteins into families, with families grouped into superfamilies and divided into subfamilies. As with species, there are multiple ways of organizing proteins. This is well illustrated by research on the nuclear hormone superfamily. This group of 48 proteins in humans is divided into families according to several different schemes. One scheme focuses on structural criteria, location of activity, and mode of function. Another scheme focuses on the functions of the cells in which proteins are expressed, while a third emphasizes evolutionary homology. In this case there is little controversy about which system to use, but the fact that biologists appeal to whichever system is most useful for a given purpose reveals the complexity of the order that has been established.

Medical practitioners have long found it valuable to categorize pathologies so as to facilitate diagnosis, conduct research, and organize treatments. In psychiatry this has generated considerable controversy, especially when the widely used categorization system, the *Diagnostic and Statistical Manual of Mental Disorders* or DSM, is undergoing revision. The reason for this is in large part that the categories are even more clearly conventional than those employed for organisms or proteins and there are few clear principles for including or excluding categories within the system. For example, the first two major editions of DSM, in use from 1952 to 1974, included homosexuality as a bona fide pathology. It was excised in DSM III in the wake of a widespread antipsychiatry movement in the late '60s and attendant protests from the gay rights community. Classifications are also frequently added, including ones that expand the domain of the pathological to include common behavioral variations like shyness and grieving, whose construal as pathologies has sometimes coincided with the approval of new psychopharmaceuticals ostensibly treating those conditions. In the preparation of the most recent version, DSM V, compulsive shopping and internet addiction were proposed as new categories of pathologies. Deleted, though, was the separate classification of Asperger's Syndrome and other Pervasive Developmental Disorders (PDDs) in favor of a single category of Autism. It is difficult to see how the deliberations over the DSM could be construed as identifying "nature's joints" (to use Plato's metaphor for finding nature's true divisions), when they appear to depend so strongly on acceptance of particular, contingent ways of living or decisions about what behaviors should be treated.

It should be clear at this point that classification systems do provide order but that scientists classify for different reasons – depending on their purposes, methods, and objects of investigation—and consequently there are multiple different

categorization systems in use. Taxonomies are not just bean-counting, nor are they mere semantics, stipulating linguistic usage. On the contrary, taxonomies and the categories on which they rest often reflect substantive theoretical commitments or methodological approaches. Cladistics, for example, prioritizes the descent relationship above all other forms of biological relationships while phonetics tries to remain non-committal. Taxonomies both influence, and are in turn affected by, the broader theoretical commitments of scientists. As with psychiatric conditions, taxonomies can sometimes be affected by social concerns about the consequences of classification. From these examples we see that biologists both find order in nature but that the order that they find is often complicated and influenced by their own interests and objectives.

3. Explaining in terms of mechanisms

One most expects to find order in science in the explanations it offers for the phenomena within its purview. Indeed, the explanatory pursuits of biologists have revealed a degree of order sufficient to ground robust scientific inquiry. But that order is very different than suggested by the popular picture of Newtonian science in which a few simple principles are portrayed as accounting for a wide range of phenomena. Rather, the order is more like that found in the design of human artifacts, where initially simple designs for accomplishing a desired result are modified over time until extremely baroque and not easily understood designs result. A corollary of this process is that initial reductionist aspirations to explain biological phenomena in terms of chemical and physical processes are complemented by much more holistic perspectives that focus on how physical and chemical constituents are integrated into systems as a result of evolutionary modifications.

The term *law* seldom figures in explanations in biology; instead, biologists frequently appeal to mechanisms when offering explanations. The conception of mechanism at work in biology grew out of the ideas of the mechanical philosophy of Descartes and Boyle but quickly expanded beyond the limitation of push-pull interaction of component parts to include processes such as chemical reactivity. Recently a number of philosophers of science whose focus is on biology have tried to articulate the key ingredients in mechanistic explanation in biology. Their accounts of mechanism have paralleled the developments in biology. Scientists begin by proposing what we call *basic mechanistic explanation* which emphasize the identification of the mechanism responsible for a given phenomenon and decomposition of the mechanism into its component parts and operations. To account for the phenomenon, though, researchers must also recompose the mechanism to show that the parts and operations together can produce it. If the organization is sequential, researchers can mentally rehearse the functioning of the mechanism. However, in the course of further investigation (initiated, e.g., to overcome inadequacies detected in the initially proposed mechanism)

researchers often find that the mechanism that they are investigating employs non-sequential organization. To understand the functioning of such mechanisms researchers must supplement basic mechanistic explanations with computational modeling of their dynamical behavior, resulting in *dynamic mechanistic explanations*. In either case, the decomposition is followed by an attempt to understand the part in the context of the whole. Surprisingly, biological explanation requires adopting both a reductionist and a holist perspective.

We begin with the reductionistic aspect of mechanistic explanation. Human-made machines require appropriate parts, and a major task in explaining a biological phenomenon is to identify the appropriate parts and the operations they perform. Since biologists are not designing mechanisms but discovering them, they require strategies for decomposing the mechanism they are investigating into their parts and operations. Typically they are not obvious; the scientist must develop ways to intervene on the mechanism so as to reveal the parts and operations. To illustrate this, consider the phenomenon, fundamental to all living organisms, of building their bodies out of nutrients they take in. One important type of part they must construct are the multitude of proteins that facilitate the many chemical reactions that occur in organisms. Uncovering the components of the responsible mechanism was a major accomplishment of the 1950s and 1960s, a project set in motion by the discovery that genes consist of DNA and that particular sequences of DNA specify the individual amino acids that are sequentially linked together to make proteins. The explanatory challenge was to identify the components of the mechanism that mediated between a sequence of DNA and the protein. These turned out to be different forms of RNA each of which was shown to perform a different operation. One can understand the basics of how the mechanism works by following the sequence of operations show in Figure 2. First, as shown in the upper left, an RNA polymerase separates the two strands of DNA and transcribes the sequences of nucleic acids on one strand into a complementary strand of messenger or mRNA. The mRNA is then transported to the ribosomes in the cytoplasm, shown in the lower part of the figure. The ribosomes are composed of another type of RNA, ribosomal or rRNA, that forms a structure on which yet a third type of RNA, transfer or tRNA, can dock to a triplet of nucleic acids on the mRNA. The tRNA consists of a unit that can combine to the three-nucleic acid sequence of mRNA and another that binds the corresponding amino acid. As the tRNA docks on the mRNA, the amino acid it ferries is added to a string of amino acids that constitutes the protein. The mRNA sequence is thus translated into a protein.

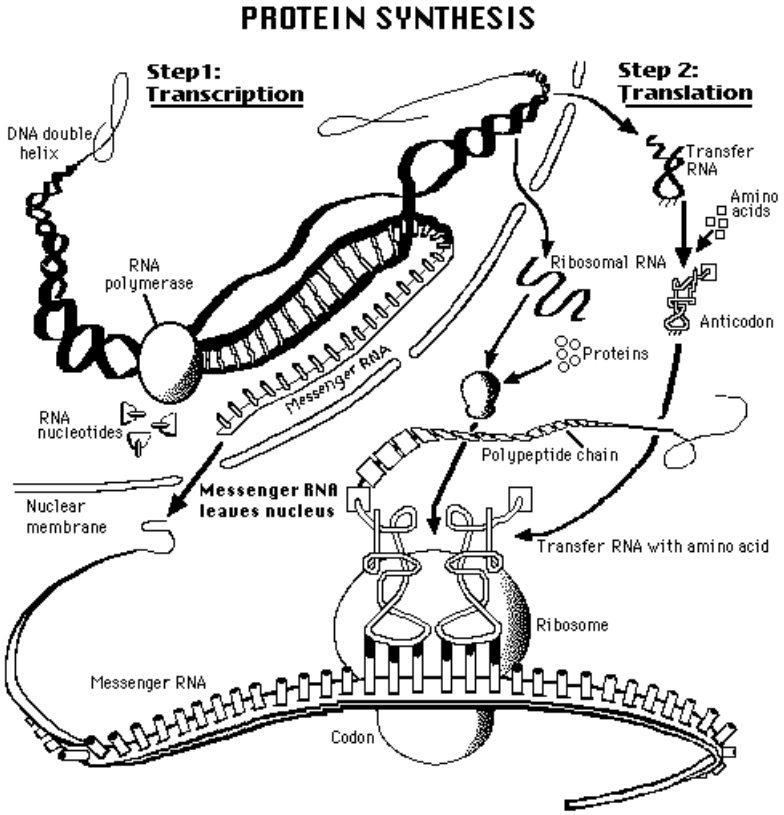


Figure 2. Basic steps in protein synthesis. Transcription of a segment of DNA into mRNA occurs in the nucleus. After the mRNA is transported to the ribosome in the cytoplasm, tRNA brings amino acids to dock at successive sites; the amino acids are then strung together into polypeptide chains that constitute the proteins. Figure in the public domain from Genentech's Access Excellence.

This account of the mechanism of protein synthesis is characteristic of mechanistic explanations in that it identifies a number of parts and the operations they perform and specifies how they are organized so that the performance of the different operations generates the phenomenon (the synthesis of the amino acid sequence that constitutes the protein specified in the DNA). Such an explanation is reductionistic in that it explains the phenomenon in terms of component parts and operations of a mechanism. We characterize such an explanation as basic because the organization is limited to the spatial location of the components and the sequence of operations we described. While identifying such mechanisms is an important accomplishment in science, often research on the mechanism reveals that the organization is not sequential and components interact in non-linear fashion. A linear interaction can be characterized using only equations that sum terms for different components and so can be graphed as a line. Any more complex relation, such as multiplication or raising a number to a power, is not linear. Determining the behavior of non-sequentially organized mechanisms of non-linearly characterized operations typically requires developing an appropriate

mathematical representation of the mechanism that can be employed in a computer simulation to determine how the mechanism will behave. The resulting explanations are what we call *dynamic mechanistic explanations*.

Further research on protein synthesis reveals non-sequential features of the way the overall mechanism is organized. For example, whether a given gene is transcribed into mRNA depends on whether the appropriate transcription factor binds to the promoter region of DNA just upstream of the part that is transcribed. Transcription factors are other proteins that are generated from other portions of the DNA so that individual genes modulate the expression of other genes. The interaction of transcription factors often involves complex networks. Even in the bacterium *E. coli*, among the simplest organisms currently living, the network through which transcription factors interact is enormously complex. Figure 3 shows about 20% of the interconnections between transcription factors in the bacterium *E. coli*—individual transcription factors are shown as circles and the existence of a line between two transcription factors indicates that one modulates the other.

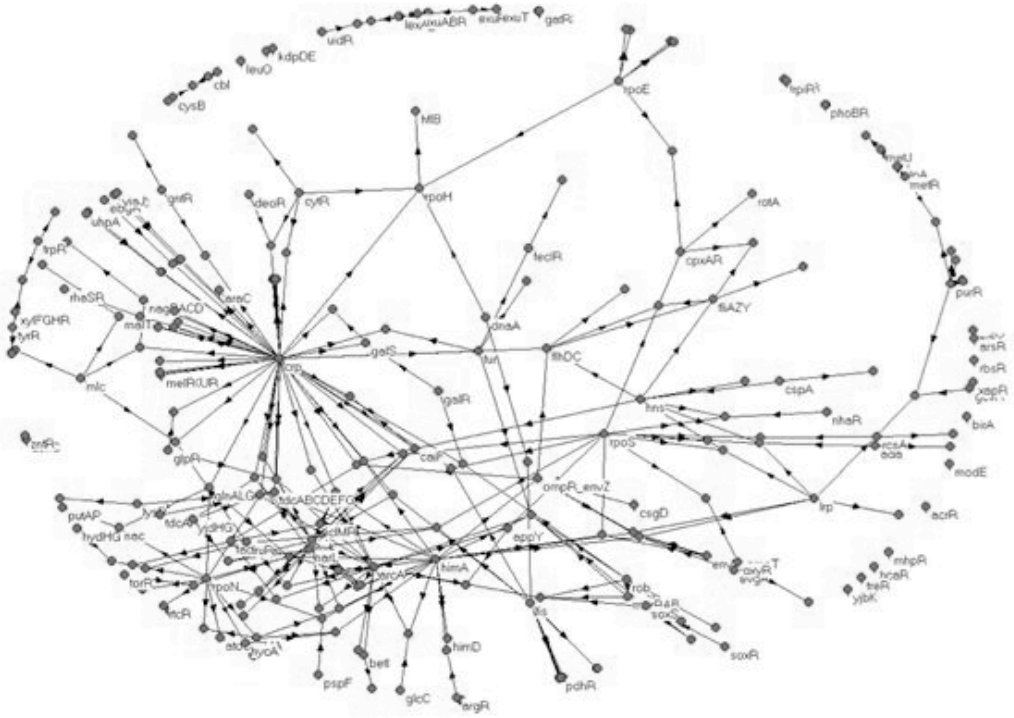


Figure 3. Network showing about 20% of the interactions in the transcription network of *E. coli*. Transcription factors are shown as open circles and lines with arrows reflect the action of one transcription factor on another. Figure by Professor Uri Alon, who kindly has provided permission to republish it here.

Figure 3 is an exemplar of the representations of complex networks that increasingly are portrayed in biological texts. A cursory examination makes clear that one cannot simply follow a sequence of reactions to understand how the whole mechanism operates. Figure 3 and its ilk seem rather disordered. There are, however, patterns of organization or motifs among small numbers of units in Figure 3 that can be explained relatively intuitively (although a fuller understanding requires mathematical analysis). Consider the feed-forward loop motif shown in Figure 4 in which there is one input from signal S to the mechanism for expressing gene X. There are two pathways from X to Z, one direct and one through Y. Assume the protein produced by X enhances expression of genes Y and Z, and the protein produced by Y also enhances Z. As long as expressing each gene takes approximately the same amount of time, and enhancing expression of Z require inputs from both X and Y, the result is a network that delays production of Z until S has been present for sufficient time for Y to accumulate. This is useful if, as is common in biological systems, there are random fluctuations in S which would, on their own, randomly generate some unnecessary product. The motif serves as a persistence detector that prevents wasteful synthesis of proteins (an energetically expensive process). Considerable recent research has been directed at identifying such motifs and determining how they behave.

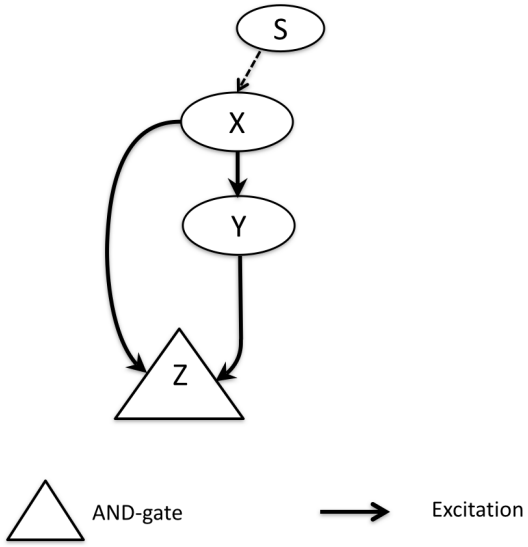


Figure 4. A simple organizational motif among transcription factors represented in Figure 3 which serves to generate Z only when the input signal S to X is persistent.

An organizational motif that is common and important in many biological networks is a feedback loop such as that shown in Figure 5, in which a gene is transcribed into its mRNA and translated into its protein, which then inhibits the initial transcription process. This arrangement is known as a *transcription-translation feedback*

loop. While on first appearances this may appear to be a strange form of organization (one might wonder why a protein should be synthesized just to inhibit its own synthesis), it has the important property of being able to generate oscillations: For a period the concentration of the protein will increase, but once its concentration reaches a sufficient level, it will block its own transcription and its concentrations will decrease until enough Z is broken down to allow X to begin to transcribe more Z again. Under appropriate conditions, a transcription-translation feedback loop can maintain oscillations indefinitely (provided a sufficient source of energy is available). In biology, oscillatory mechanisms are often employed to segregate in time activities that interfere with each other. One of the best known is the oscillatory mechanisms involved in circadian rhythms . Just as we use external clocks to distinguish times for work, meals, and pleasure activities, organisms employ clock mechanisms built from feedback loops to temporally segregate the activities they must perform, some of which are incompatible with others. We experience the power of these mechanisms when they are disrupted as in the phenomenon of jet lag—one consequence of jet lag is increased susceptibility to diseases, which results from our immune system providing protection at a time when exposure to pathogens was greatest at our previous location but not in our new time zone.

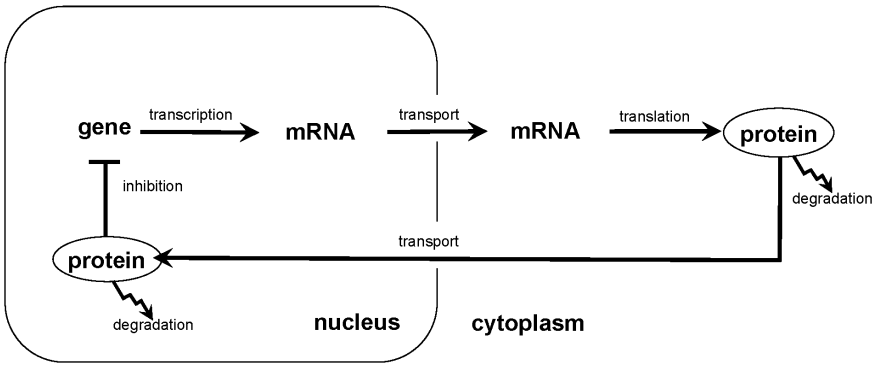


Figure 5. Schema of a transcription-translation feedback loop in which a protein synthesized from a gene serves to inhibit its own transcription until it degrades sufficiently to allow synthesis to begin again.

We have offered two examples, both relatively simple, in which the non-sequential organization of the mechanism results in more complex behavior than possible with sequential organization. In both cases, a detailed understanding of how systems organized in these ways requires mathematical analysis (for example, sustained oscillations in feedback systems require that the component operations be non-linear in appropriate ways) and hence dynamic mechanistic explanation. We conclude this section with reflections on the implications of the increasing prevalence of dynamic

mechanistic explanations in biology for order in biology. The reductionist perspective of basic mechanistic explanation sought order by identifying the components of a mechanism and showing how the phenomenon of interest resulted from the sequential operation of these components. The recomposition of the decomposed mechanism required little more than the sequential rehearsal in the scientist's mind of the component operations. But the discovery that biological mechanisms often violate sequential order and that the operation of individual parts are affected by their place in complex networks requires scientists to focus on how whole mechanisms are organized and how they are situated in a larger environment that manifests similarly complex organization. Researchers have often found that networks exhibit *small-world organization* in which, although there are local modules of components, there are also short pathways through which activity in different modules can affect activity within each . In recomposing the results of efforts at decomposing mechanisms biologists must bring a holist perspective to complement the reductionistic perspective from which they began. The resulting order provided by biological mechanisms is far more baroque than that to which biologists aspired—the emerging picture is one in which there is not only a different mechanism for each phenomenon but each mechanism is affected by all of the others in the cell, organisms, or ecosystem in which is functions. To explain biological phenomena, biologists must be reductionists and holists too.

4. Descent with modification

The theoretical biologist Theodosious Dobzhansky famously remarked: "Nothing in biology makes sense except in light of evolution." One way evolutionary theory helps make sense of biological phenomena is by viewing current life forms as the product of descent with modification. Through much of the 19th century, many scientists viewed Darwin's main accomplishment not as establishing natural selection, but as establishing that today's organisms descended from earlier ones. This has provided a crucial ordering principle for many biologists. But as we show, it rests to a large extent on the assumption of vertical inheritance: passing traits from one generation to another. That assumption is now being substantially hedged due to the newfound appreciation of horizontal inheritance, the passing of traits between organisms from different lineages, which could render descent with modification as merely one part of the biological toolkit, rather than a general principle.

Prior to Darwin, comparative anatomists focused on structural similarities between organs in different organisms, dubbed *homologies*. An important clue to whether two traits were homologs was whether they appeared alike in early stages of development. Traits that developed early, scientists reasoned, were more likely to be general characteristics shared amongst organisms of a given kind, with specific differences arising later in development. With the adoption of the evolutionary

perspective of descent with modification, traits were construed as homologous when they arose from the same trait in a common ancestor.

The scope of application for homology has since broadened: processes and functions can be homologized, and in the wake of molecular biology, genes and proteins are homologized as well. After genes were identified as sequences of DNA, geneticists and molecular biologists characterized proteins as homologous when the DNA sequences that encoded them were descendent from a common ancestor. Such sequences are also referred to as *conserved*, and many of the basic genes involved in either metabolism or gene expression appear to have been conserved from bacteria and archaea to mammals, including humans.

An example of conservation is found among the peroxiredoxin enzymes that evolved in archaea and bacteria to bind and use oxygen. Following the advent of photosynthesis on Earth about 3.5 billion years ago and the accumulation of atmospheric oxygen it produced, it was highly advantageous to be able to bind this reactive oxygen molecule, essentially a poison because of its ability to disrupt other cellular processes. The amino acid sequence for peroxiredoxins (Figure 6) is virtually the same for many organisms from bacteria to humans, with a few differences in regions beyond the active site. These enzymes have been so strongly conserved presumably due to their usefulness for all organisms in oxygenated environments.

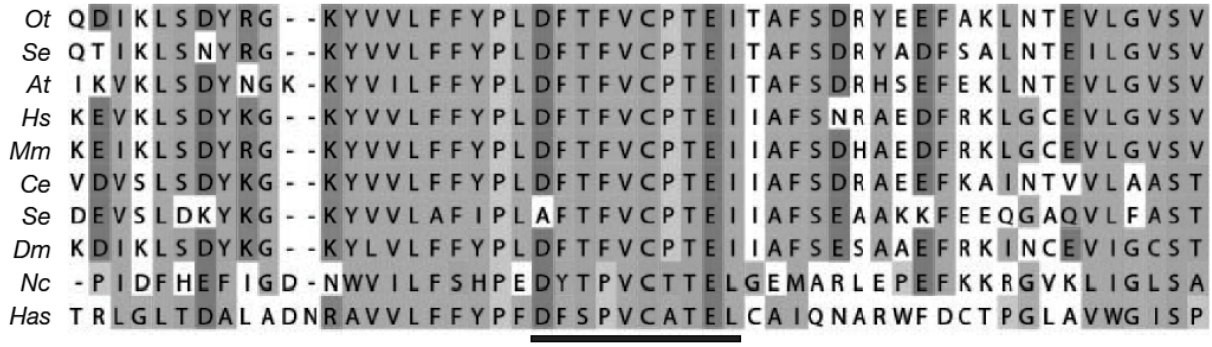
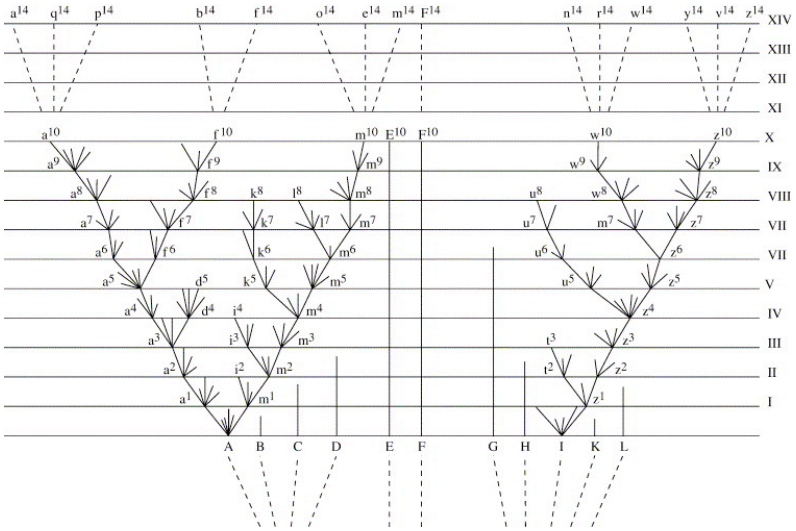


Figure 6. Peroxiredoxin amino acid sequence map. The active site is shown by the black bar, on bottom. Sequences are shown for several Eukaryotic species (At, A. thaliana; Ce, Caenorhabditis elegans; Dm, D. melanogaster; Hs, Homo sapiens; Mm, M. musculus; Nc, N. crassa; Ot, O. tauri; Sc, S. cerevisiae) and one species each of Bacteria (Se, S. elongatus sp. PCC7942) and Archaea (Has, H. salinarum sp. NRC-1). Reprinted with permission from Reprinted by permission from Macmillan Publishers Ltd: Nature (Edgar, Green, Zhao, van Ooijen, Olmedo, Qin, Xu, Pan, Valekunja, Feeney, Maywood, Hastings, Baliga, Merrow, Millar, Johnson, Kyriacou, O'Neill, & Reddy), copyright 2012.

One of the major reasons biologists are interested in homologies is that they undergird a powerful research strategy—conducting research on one organism to

understand another. For example, much bio-medical research ultimately directed at humans is actually done on rodents. The reasons for this are not just ethical—researchers prefer to study a mechanism in the simplest organism in which it appears. But this requires a standard for determining when a studied organism possesses the same mechanism, and homology provides this standard.

Descent thus provides an important ordering principle. This process of descent and diversification was captured in the representations of a tree of life, illustrated in the only figure Darwin included in the *Origin of Species* (Figure 7, top): each species is shown as a node on a branch splitting from one root. But the traditional account of vertical descent from parents to offspring, which underlies the tree metaphor and in some cases the tracing of homologous traits back to common ancestors, is being increasingly subjected to challenge.



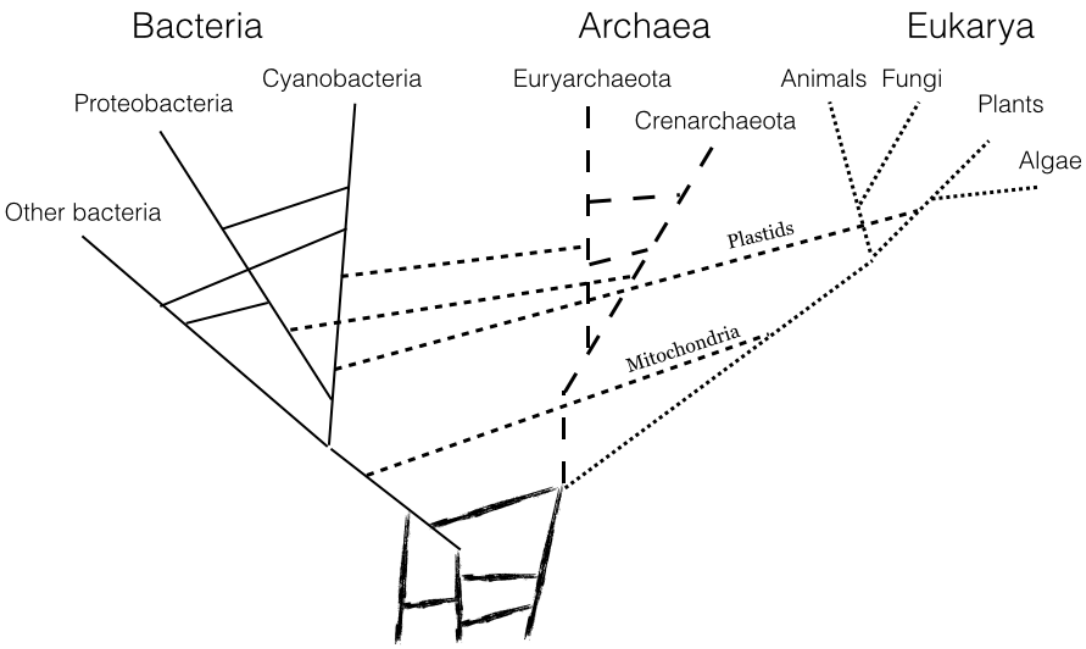


Figure 7. Representation of descent with modification in tree diagrams. Darwin's representation of the tree of life (top) shows all descent as vertical—new species split from existing ones. Revised tree that captures the suggestion of abundant horizontal gene transfer (bottom).

On the traditional view, each organism receives DNA just from its parents and passes it on to its offspring; DNA is not shared between organisms. In the mid-20th century, though, research on microbial drug resistance showed that bacteria could pass genetic material between themselves and other organisms, not only to offspring, a phenomenon known as horizontal or lateral gene transfer.

Although initially a curiosity, horizontal gene transfer has become recognized as a major factor in the ability of bacteria to resist antibiotics. If one species of bacteria in an environment has a mechanism for combating a drug, it is quickly transferred to those on which the drug was targeted. And this phenomena is not limited just to drug resistance – the more scientists look, the more horizontal gene transfer they find. In fact, it is not limited even to the world of bacteria. The ability of plants to photosynthesize is thought to be the result of an ancient fusion of photosynthetic bacteria with larger and more complex cells, which together made the first plant cells. Likewise, the ability of your body cells to produce energy, it is now hypothesized, is the result of ancient bacteria adapting to life within larger cells, and over time the bacterial portion developed into what we now know as mitochondria, the crucial "power plants" within cells. These two cases of *endosymbiosis* are another kind of horizontal transfer, insofar as genetic information was not strictly confined to parent-offspring relations, but actually became part of the larger organism. Horizontal gene transfer is now recognized as a major factor

in the evolution of every branch of life. Moreover, the mechanisms that facilitate horizontal gene transfer enable organisms to perform a variety of operations on their own genome, moving genes to locations that suppress or increase their expression and recombining genes in ways that support the creation of novel proteins out of existing components, processes that further challenge the ability to understand conservation as a relatively simple process of descent with modification.

There is some dispute about the frequency of horizontal transfer, and the degree of challenge it presents to the traditional tree of life. Some argue that it is sufficiently rampant that the tree of life metaphor should be rejected; others argue that it adds a few cobwebs to the tree but that the basic tree structure can still be deciphered. We do not take a stand on whether horizontal gene transfer is devastating for reconstructing the tree of life, but rather emphasize that at the very least, it complicates the analysis of descent and the attempts to understand the conservation of mechanisms. A mechanism may be conserved either from a common ancestor in a vertical tree or from an unrelated organism in a different phyla.

5. Conclusion

We have identified three types of order biologists have found in nature, but none of these yields a neat, ordered picture that many have hoped for. In particular, simple laws with wide explanatory power do not seem to be in the offing. While some early evolutionists, including Darwin himself, initially referred to natural selection as a "law," that label is no longer commonplace. Darwin seems to have conceived natural selection as a universal force acting everywhere at all times. On that view, it would be like some novel Newtonian force, always present in the same way even if its effects varied between individuals. Today natural selection is conceived more as a long-term statistical summary of many disconnected individual facts relating organisms' variation, reproduction, and environments. Natural selection is typically referred to as the "mechanism" of evolution, but not necessarily in the same sense as the mechanistic explanations discussed above.

There is good reason not to expect in biology the sort of universal order that is putatively provided by Newtonian laws. Living organisms have only been identified in a very small portion of the physical world where they appear to have descended through a process of descent with modification in specific environments (even if the process is not totally vertical). Moreover, even if life is found elsewhere in the universe, it is likely, just as life on Earth, to reflect its historical development in a particular location. Whatever biological order is to be found should be expected to be piecemeal and local compared with that provided by any all-encompassing laws. Lacking general laws that might organize the discipline, biology nonetheless employs a number of ordering principles such as the three we have identified. On first appearances, each seems to

provide a fairly straightforward mode of order. But in each case we have seen that the order is more complex than first thought.

In retrospect, it often seems easy to identify the oversimplifications of earlier research programs. Descartes' proposed philosophy of biology appears quite crude to modern biologists. Yet, life sciences evince patterns of inquiry in which initially simpler theories are used to investigate phenomena, and which then give way to increasingly rich details, until the original theory is perhaps no longer even explicitly upheld. For example, early organism taxonomies involved comparing general similarities, which later yielded a multiplicity of dimensions of comparison. Or alternatively, the attempt to decompose biological mechanisms is often attended with dangers, which were sometimes astutely pointed out by 19th century vitalists, but a combination of reductive and holistic scientific strategies eventually supplanted many of the initially simplistic mechanisms proposed. This pattern shows little sign of ending or final culmination: while some physicists search for a "final theory" which will unify and make sense of the myriad phenomena they study, there is slim hope of such a universal explanations in the life sciences.

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