

PERSPECTIVES



Conceptual foundations of evolutionary thought

K. P. MOHANAN*

Indian Institute of Science Education and Research, Pune 411 008, India

*E-mail: mohanana@iiserpune.ac.in.

Received 23 January 2017; revised 9 March 2017; accepted 13 March 2017; published online 4 July 2017

Keywords. evolution; symmetry breaking; emergence; constraints on evolution; biological and cultural universals; transdisciplinary conceptual inquiry.

This article seeks to explore the conceptual foundations of evolutionary thought in the physical, biological, and human sciences. Viewing evolution as symmetry breaking, it explores the concepts of change, history, and evolutionary history, and outlines a concept of biological macroevolution as the emergence of novel distinctions in both taxa and traits. It then generalizes the concept to physical and cultural evolution, and pursues the consequences of the definition to the emergence of structures, systems, and functions, as well as to the evolution of constraints on these aspects of organization.

Introduction

In any field of study, it is important every so often to step back from details and return to the foundational issues of the field. The exploration of the foundations of mathematics involves

... the study of the logical and philosophical basis of mathematics, including whether the axioms of a given system ensure its completeness and its consistency. Because mathematics has served as a model for rational inquiry in the West and is used extensively in the sciences, foundational studies have far-reaching consequences for the reliability and extensibility of rational thought itself. (Encyclopedia Britannica <https://www.britannica.com/topic/foundations-of-mathematics>).

The term ‘foundations’ is not so widespread in the physical and biological sciences. However, generalizing from the concept of foundations in mathematics to a broad concept of foundational studies, we could ask questions on the

foundations of physics, biology, linguistics, and the study of human history.

We might think of foundational studies as being composed of two strands, namely the formal (or ‘logical’) and the conceptual (or ‘philosophical’). Russell and Whitehead’s *Principia* would then fall under the study of the formal foundations of mathematics. Investigating the formal foundations helps us maximize the rigour of proofs and calculations.

In contrast, when we ask questions like ‘What is the object of inquiry in mathematics?’, ‘What is a mathematical proof?’, or ‘How is a mathematical proof distinct in its grounds and reasoning from scientific proofs and legal proofs?’, we are exploring the *conceptual* foundations of mathematical *inquiry*. And when we ask, ‘What is number?’ ‘What is space?’ and ‘Is Euclidean geometry a special case of topology?’ we are exploring the conceptual foundations of *knowledge* in mathematics. Investigating the conceptual foundations guides us to meaningful questions and new paths to look for answers. This in turn strengthens the substantive (nonformal) components of theories.

In biology, ‘What kind of mathematical formalism should we use to calculate the sum of advantageous and deleterious effects of the same mutation?’, ‘What formalism should we use to calculate the distribution of trait values over time?’, and ‘Is the species concept best modelled as a crispy set, a fuzzy set, or a prototype set?’ are formal questions. In contrast, questions like ‘What is life?’, ‘What is a living organism?’, ‘What is a species?’, and ‘What criteria allow us to decide whether a given node in the tree of life is a kingdom or a phylum?’ are conceptual questions (see point 1 in appendix).

In this article, I seek to explore the conceptual foundations of evolutionary thought in the physical, biological, and human sciences. Drawing on the mathematical concepts of transformation, symmetry, and symmetry breaking, section 2 defines evolution as symmetry breaking. It unpacks the concepts of change, history, and evolutionary history; outlines a concept of biological macroevolution (not extendable to microevolution) as the emergence of novel distinctions in both taxa and traits; and generalizes the concept to physical and cultural evolution. Section 3 pursues the consequences of this definition of evolution to the emergence of structures, systems, and functions, and evolving constraints on these aspects of organization.

What is evolution?

Evolution is a special form of history. To understand evolution as a specific trajectory of history, we must begin with the concept of change, and then ask what forms of change distinguish evolution from mere history (see point 2 in appendix).

Change

Change is best understood in terms of *shared* and *distinct properties* along the parameter of time. If we were shown two identical dots on a piece of paper, and asked to differentiate between them, we would identify their locations as different. But if we were told that it is the same dot, we would describe the same reality as change of location: the dot has moved from one location to another. Likewise, if we were asked to compare and contrast two photographs, we would formulate our observations in terms of the properties they share, and the properties that distinguish them. If we were now told that they are photographs of the same person at two different times, we would formulate the same observations in terms of change.

Thus, *change* may be viewed as distinctness in the properties of an entity along the dimension of time. This implies the *persistence* of a set of properties shared across the different points of time. Persistence and change are thus two sides of a coin; and so are their equivalents, *sharedness* and *distinctness*, and also, *invariance* and *variability*.

Transformation, symmetry, and symmetry breaking

Variability and invariance, counterparts of change and changelessness in term of time, correspond to transformation and symmetry in the vocabulary of mathematics. Transformation is a change in some properties while some others remain unchanged. Rotation, for

instance, is a transformation that changes the orientation of an object without changing its size, shape or location. Translation is a transformation that changes its location without changing its size, shape or orientation. Scaling (enlargement or reduction) changes the size without changing the shape. Topological transformations change shape as well, but retain continuity (without breaks or holes).

When viewed as change, a transformation of an entity from X to Y involves a set of properties shared between X and Y, and a set of properties distinguishing X from Y, with X preceding Y along the parameter of time. If we remove the time element, a transformation is a relation of sameness (what X and Y share, the symmetry) and distinctness (what distinguishes X and Y). Hence, instead of viewing transformation as an operation (with a process metaphor), we might describe it as *variability under invariance*. Symmetry, then, is the equivalence relation of *invariance under variability*. It then becomes clear that the concept of homology in biology, when expressed independently of evolution and ancestry, is the same as symmetry. When we say that the arms and legs of humans are homologous to the arms and legs of chimpanzees and the wings of bats, we are saying that a relation of symmetry devoid of the temporal metaphor of transformation, holds among them.

It is therefore not surprising that D'Arcy Thompson (1942) sought to capture the homological relations between the skulls of different organisms in terms of topological transformations (if we reintroduce temporality into transformations, the 'input' to the operation is the proto-form, and the output is the evolved form).

Symmetry is what remains invariant after a transformation. If we take a square whose corners are labelled ABCD and rotate it by one right angle, its initial state and final state are indistinguishable except for the labels, so we say that they are symmetric. In homology, those aspects that persist from the proto-form to the evolved form constitute symmetry, while those that distinguish the different evolved forms constitute results of transformation. This corresponds to what Darwin called descent with modification.

When a square undergoes one full rotation, there are four orientations that are nondistinct. Hence, we say that it has a rotational symmetry of four. An isosceles triangle has a rotational symmetry of three; a regular pentagon of five; and a regular octagon of eight. A circle has perfect (infinite) rotational symmetry: when it is rotated, there are no orientations that are distinct. If we now change a circle into a regular hexagon, we have broken its infinite symmetry: when a hexagon is rotated, a distinction in orientation appears. It now has a rotational symmetry of six, instead of infinite symmetry. Thus, *symmetry is the absence of distinctions, and symmetry breaking is the emergence of a distinction*.

Evolution as symmetry breaking

Physicists assume that time and space came to exist in our universe at the point of the Big Bang. At that point, before fundamental particles were born, the universe must have been without distinctions. This perfect symmetry was broken by the emergence of distinct fundamental particles. The *types* of particles that emerged at that time persist today, regardless of the birth and death of *particular* particles. The next stage in the evolution of the universe was the emergence of diversity at the level of atoms, followed by that of molecules. The emergence of galaxies, stars, and planets constituted evolution at the level of the large. (What is important for our purposes is the emergence and persistence of differentiation, not the emergence of a particular entity belonging to a preexisting type).

The history of life is an example of the same pattern of symmetry breaking and persistence. From the undifferentiated category of prokaryotic organization emerged the differentiation between prokaryotic and eukaryotic. From the unicellular emerged the distinction between unicellular and multicellular. Then emerged the distinction between organizations with and without tubes, with and without vertebra, with and without a neocortex.

In the history of humanity, we find the emergence of man-made objects including tools and utensils, made of stone, and then of metal. There is the emergence of writing, money, science, formal education, banking, the notion of 'state' and 'nation', and a vast range of industrial products and services. All these are instances of symmetry breaking, and the persistence of the emergent traits.

Given this picture, it would be useful to define the transdisciplinary concept of evolution—holding on the physical, biological, and human worlds—as history that involves symmetry breaking and persistence. It can be formulated as

the history of the emergence of diversity (novel distinctions) and the persistence of the emergent, typically accompanied by increased complexity of organization.

As stated earlier, this is a proposal for a definition of macroevolution. Microevolution is a change in the distribution of the trait values in a population without necessarily involving an emergence of novel traits or trait values; hence the definition is not applicable to microevolution.

Towards an integrated theory of biological and cultural evolution

Two strands of biological evolution

Some foundational concepts and statements of the academic world tend to have a significant impact on the concepts and statements of ontology, in terms of the

nonspecialist worldview. When examining foundational questions, it is useful to identify those central concepts and statements. To illustrate, the heliocentric theory of the solar system, and the atomic theory of matter, are two of the most important features of the 'modern' worldview. The central theses of these two theories can be stated as:

Heliocentric theory: Contrary to earlier thought, the earth is not the stationary center of the universe. It revolves around the sun (like other planets) and rotates on an axis tilted to the plane of revolution.

Atomic theory: Contrary to what Aristotle thought, matter is not infinitely divisible. All matter is made up of molecules; molecules are made up of atoms, and atoms are made up of indivisible particles.

The central thesis of the modern theory of biological evolution might be formulated as:

Theory of biological evolution version 1: All existing and extinct species on the earth evolved from a single unicellular ancestor species. (It is not the case that the existing species have existed forever, or that each species has evolved from its own distinct unicellular ancestor species.)

This version is formulated in terms of the concept of 'species', calling for a testable definition of the concept. An alternative formulation might be in terms of the concept of phenotypic traits. (In what follows, unless otherwise specified, I will use the term 'trait' only to refer to organismic and cultural traits.) A trait such as eye colour or number of legs is a variable, or a feature. The value of the trait of eye colour in humans can be black, brown, gray, blue, or green. Likewise, the value of the trait of number of legs can be zero, two, four, six, eight, etc. Using the concept of 'trait', the central thesis of the modern theory of biological evolution can be formulated as:

Theory of biological evolution version 2: All existing and extinct traits and trait values of biological organisms on the earth evolved from the traits and trait values of a single unicellular ancestor (or a single population of unicellular ancestors).

Both these discipline-specific formulations of biological evolution are consistent with the transdisciplinary definition of evolution proposed earlier, as *the history of the emergence of diversity (novel distinctions) and the persistence of the emergent*. (As will become clear in a subsequent section, evolution of traits presupposes a conception of a hierarchical structure among traits and their values, analogous to the hierarchy of biological taxa in the 'tree of life'. Hence there is no contradiction in the concept of novel traits evolving from ancestral traits higher up in the tree.)

The difference between the two versions is this. Version 1 is concerned with the *diversity of groups of organisms* (taxa, including species and subspecies). It views evolution

as the appearance of novel nodes in a phylogenetic tree of life. Topics such as ‘evolution of insects’ and ‘evolution of primates’ provide research questions within this version. Version 2 is concerned with the *diversity of traits*. This version of evolution can also be expressed as the appearance of novel nodes in a hierarchical tree that represents the structure of traits. In this version, topics that provide research question would include ‘evolution of the eye’ and ‘evolution of flight’.

The transdisciplinary definition of evolution proposed here unifies the discipline-specific concepts of evolution in the three domains: physical, biological and cultural. But such integration also needs to be supplemented by differences across domains. The properties that yield the distinctions among them are:

- Inheritance, lineage, and selection (these appear in biological and cultural evolution but not in physical evolution); and
- Reproduction in terms of parents and offspring (this appears in biological evolution but not in physical or cultural evolution).

In addition to *downward* inheritance (from one generation to the next), cultural inheritance can also be *horizontal* (across peers in the same generation), or *upward* (from one generation to the previous). However, horizontal and upward inheritances occur only when the source and target of inheritance exist simultaneously. Otherwise, only downward inheritance is possible, whether biological or cultural.

In what follows, we will focus on developing a framework for building a unified theory of biological and cultural evolution, ignoring physical evolution.

Now, the concept of evolution as the *emergence of taxa*, adopted in mainstream evolutionary theory in biology, is grounded in the species concept, and the resultant concepts of mutation, selection, fitness, inheritance, and lineage in terms of reproduction involving biological parents and offspring. While this approach is important within biology, it cannot be extended to cultural evolution. Hence, to build an integrated theory, it may be useful to pursue the concept of evolution as the *emergence of novel traits*.

Evolution as the emergence and persistence of traits

Periods of taxa and traits: Historical studies often refer to ‘periods’ (ages/epochs) such as the Cambrian Period, Jurassic Period, Paleolithic Period, Neolithic Period, Stone Age, Copper Age, Bronze Age, Ice Age, Holocene Epoch, Anthropocene Epoch, and Information Age. A period in such cases is marked by the onset of a new trait such as the making and using of stone tools in human history, or of digital technology.

Generalizing this concept of period to taxa, we may talk of animal period, insect period, vertebrate period,

bird period, mammal period, ape period, and human period in biological evolution. Since unicellular organisms, multicellular nonanimals, invertebrate animals, nonmammal vertebrates, nonape mammals, and nonhuman apes continue to exist, we may say that each of these periods persists in the history of life on earth (this is not to say that all periods persist. The dinosaur period, for instance, has not continued to the present. As a result, the combination of beaks and teeth no longer exists in current life forms on earth).

We may also acknowledge periods whose onsets are marked by the emergence of a trait. Thus, within the concept of evolution in terms of the diversification of traits, we can talk of the sexual reproduction period, the wing period, the eye period, the red blood period, the neocortex period, and so on. Likewise, we can think of the writing period, printing period, email period and smart phone period in the history of humanity.

Traits and trait values, entities, structures, and systems: To place in a transdisciplinary perspective the ideas of the evolution of traits and of taxa, it would be useful to unpack the concept of *trait*, and other concepts related to it. Consider the following examples of the distinction between traits and trait values:

	Trait	Values
a)	Leghood	Has legs / does not have legs
b)	Number of legs	1, 2, 3, 4, 5, 6, 7, 8, ...
c)	Featherhood	Has feathers / does not have feathers
d)	Feather colour	Black, white, brown, yellow, orange, red, purple, blue, ...
e)	Eyehood	Has eyes / does not have eyes
f)	Eye colour	Black, brown, green, blue, gray, red, yellow, purple...
g)	Eye compoundness	Compound / noncompound
h)	Beakhood	Has beak / does not have beak

A ‘trait’ is a variable whose values may be gradient or discrete. If discrete, a trait may have two or more values (see point 3 in appendix). For example, ‘leghood’, as indicated above, is a binary-valued trait. Organisms that have the trait ‘has legs’ have a further trait, ‘number of legs’. This trait has ‘bipedal’, ‘tetrapod’, and so on as its values. This suggests that traits and trait values have a hierarchical structure, perhaps better illustrated by the structure of the trait ‘eyehood’ (figure 1).

Notice that, in the above account, legs, feathers, eyes, and beaks are entities that an organism is composed of. An entity may be atomic or complex. Fundamental particles are atomic entities in the sense that they are not composed of any parts, while atoms are complex entities composed of nuclei and electrons, nuclei being made up of further parts. At the level of chemistry, an atom is an atomic entity, and

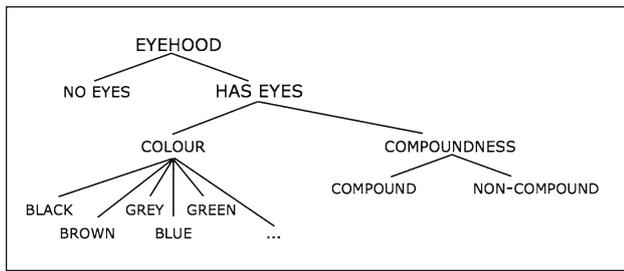


Figure 1. The hierarchical structure of traits and trait values.

molecules are complex entities made up of atoms. At the level of molecular biology, inorganic molecules are atomic entities, while DNA, RNA, and proteins are complex entities. At the level of cellular biology, molecules are atomic entities while a cell is a complex entity made of cytoplasm and a cell membrane, with an optional nucleus. At the level of organismic biology, a cell is an atomic entity, while the tissues, organs, and organisms are complex entities. At the level of society, organisms are atomic entities, while social groups like communities, societies, tribes, colonies, populations, and species are complex entities.

As with complex traits, complex entities also have a structure, a configuration of the parts that stand in certain relations to the whole and to one another. The skeleton of the human arm, the chimpanzee arm, a frog's leg, a lizard's leg, a bird's wing, a bat's wing, and a whale's flippers have distinct shapes; but they all have the same core skeletal structure that we call homology in biology, and symmetry in mathematics (see point 4 in appendix).

We may now formulate as follows the central questions to be addressed by an integrated theory of evolution that unifies evolution at the physical, biological, and societal realms, including the study of human society and human history.

Atomic and complex entities have traits, trait values, trait value combinations, structures, systems, and functions. They also have constraints on trait value combinations and on structures. And each of these has its own evolutionary trajectories. Some trait values, trait value combinations, and constraints on these combinations have evolved over time, while others have persisted without change.

- (i) *What is the nature of these trajectories? (i.e., How have they come to be the way they are?)*
- (ii) *What are the regularities that underlie the trajectories?*
- (iii) *What are the systemic forces that influence change versus persistence?*

Question (i) seeks to understand the present by looking for explanations in terms of origin and evolution; it asks for historical explanations. For instance, consider the system of taxation in human governments, or the system of

examinations in educational organizations. To understand why the systems are the way they are, we need to understand their origin and evolutionary history. Likewise, to understand why the human brain has an anatomical module devoted to face recognition, why tetrapods have brains, or why organisms that have lungs also have vertebrae, we need to understand the origin and evolution of the brain, limbs, lungs, and bones.

Question (ii) asks for the general principles—constraints or laws—that exist in the past, present and future, guiding the trajectory of evolution. For instance, in the evolution of the physical universe (Big Bang cosmology) in theoretical physics, relativity and quantum mechanics serve as such guiding principles. The basic idea here is that, in the absence of evidence to the contrary, the general principles that apply to the here-and-now also apply to the faraway in both time and space, articulated as the 'Uniformity Principle'. In evolutionary biology, Darwin adopted this principle from Lyle as the foundation for a theory of evolution (Sober 1991).

The statement that all existing and extinct species evolved from a single ancestor species, or that all existing and extinct traits with their values evolved from the traits of a single unicellular ancestor, comes under a theory that addresses question (i). In contrast, theories of fitness, random mutation, and selection, along with theories of reproduction and development, come under a theory that addresses question (ii). Notice that the way they are formulated above, both (i) and (ii) cover the evolution of both taxa and traits.

While the questions arise in the context of evolution, they are equally relevant for development; they may be taken as the central questions for an integrated theory of what has been called evo-devo, and for an integrated theory of evolution in the physical, biological, and cultural realms.

As for question (iii), we will return to it after a discussion of the role of constraints in a theory of evolution.

Constraints on evolution and development: Half a century ago, Conrad Waddington said:

Theoretical physics is a well-recognized discipline, and there are departments and professorships devoted to the subject in many universities. Moreover, it is widely accepted that theories of the nature of the physical universe have profound consequences for problems of general philosophy. In contrast to this situation, theoretical biology can hardly be said to exist as an academic discipline. There is even little agreement as to what topics it should deal with, or in what manner it should proceed. (Waddington 1968)

A central concept in Waddington's work that is relevant to the questions we raised in the previous section is that of 'epigenetic landscape'. By epigenetic landscape,

Waddington refers to that which shapes the trajectory of trait evolution, and the constraints that delimit the multidimensional trait space of biological organisms. Consider, for instance, the following correlations in phenotypic traits:

Organisms with beaks also have feathers, and vice versa.

Organisms with beaks have two legs, and no teeth.

Organisms with six legs also have compound eyes, and vice versa.

No organism capable of photosynthesis has vertebrae.

No organism has an odd number of limbs.

No organism has an odd number of eyes.

These are correlational constraints or ‘observational laws’, analogous to Galileo’s laws of falling bodies and of the simple pendulum, and the laws of ideal gases that connect temperature, pressure and volume (see point 5 in appendix). Just as in physics, these observational laws are explained in terms of theoretical models and theoretical laws at a higher level, we need to look for explanations in theoretical biology for phenotypic laws of the kind illustrated above.

One way to construct a theory of the regularities of the phenotypic trait space is to begin with development in a given species, and then generalize it to taxa. For instance, consider the cluster of laws, ‘organisms with beaks also have feathers, two legs, and no teeth’. Suppose we ask the question, ‘Why do crows have beaks?’ The answer, in developmental biology, would be in terms of a given configuration of genes that govern the formation of beaks in crows, say, *Fgf8* and WNT (and probably *SHH* as well), which seem to co-occur (Bhullar *et al.* 2015; Pennisi 2015). Now, when we move up the taxa and ask, ‘Why do crows, hummingbirds, parrots, hawks, and eagles have beaks?’ a higher-level question arises: ‘Why do crows, hummingbirds, parrots, hawks, and eagles have this configuration of genes?’

Even this is not enough. Birds’ wings point us to Hox-D 11, and to the genes for the four limb skeletal structure. And the presence of feathers points to a cluster of genes called alpha and beta keratin (Greenwold *et al.* 2014). We now translate the statement that organisms with beaks have feathers and vice versa into the following statement:

Fgf8 and WNT \longleftrightarrow alpha keratin and beta keratin.

The next step would be to look for a configuration of genes that explains why organisms with beaks and feathers also have two legs, but no teeth. This would call for constraints at the molecular level (how previous selection shapes (if not determines) the molecular level constraints would be a second order issue).

Evolutionary theory must explain the evolution of such constraints. Thus, for a fuller explanation, a theory of

development needs to be supplemented by a theory of evolution.

Search for laws in biology: Mendel’s laws, the mathematical equations of population genetics stemming from Mendel, and the work inspired by research in biology as a complex adaptive system in the Santa Fe Institute of Complexity, are examples of a fruitful search for laws in biology. In fact, the investigation of laws or constraints governing structure and processes in development and evolution in biology, as pointed out above, is at least as old as Darwin. The search for such laws has significant consequences for our understanding of persistence in evolution.

Darwin recognized the need for evolutionary thought to examine not only how some traits undergo change (mutation and selection: e.g., how light sensitive spots on the skin evolve into human eyes), but also how some traits persist (e.g., bacterial cells and human cells both have cell membranes and protein molecules; the structure of the food tube in the animal kingdom has remained stable across time, from the origin of worms to the origin of humans; and so on). Thus, change and persistence, the equivalents of symmetry and transformation in mathematics, are two sides of what needs to be explained in an integrated theory of evolution. More specifically, heredity must explain not only the similarities between parents and offspring, but also their differences, and conversely, evolution must explain not only the differences between parents and offspring, but also their similarities.

Now, motion in Newtonian mechanics is change of location, and inertia is the persistence of uniform motion (including nonmotion). In physics, both why physical objects change their velocity, and why they persist in their velocity are important questions. In exploring persistence in evolution, we are looking at the counterpart of inertia in the physical world: why some aspects of organization (traits, structures, systems, and functions) resist change in the course of evolution.

Darwin conceptualized persistence as ‘unity of type’ at the level of taxa. Under this conception, evolution builds on already existing structures, systems, and functions to yield more complex organisms. This idea is further developed in Francois Jacob’s idea of bricolage (tinkering: ‘evolution as a tinkerer’), which views the way nature works as being analogous to the way an engineer as inventor works (Jacob 1977; Racine 2014). This opens a way of understanding persistence, while Waddington’s idea of constraints governing epigenetic landscapes (Waddington 1968) shows a way of formulating what persists in the course of evolution.

Logically possible combinations of trait values yield what we may call the trait space: a multidimensional abstract space within which all life forms belong. Of this available space, life forms occupy only a small part.

Constraints on evolutionary trajectories give us a way of capturing that subspace.

Mathematics studies logically possible worlds by inventing axioms and definitions, guessing conjectures, and proving them as theorems (showing that they are logical consequences of the axioms and definitions). Science studies the particular world we live in by observing what is observable, guessing what might underlie what we observe, and proving them as theories that explain the observed patterns. One such pattern is the asymmetry between what we observe (e.g., dropped objects come down in a straight line, objects thrown up come down in a parabolic path) and what is never observed (e.g., dropped objects do not come down in a spiral or zigzag path; objects thrown up do not stop in mid-air and remain there).

From this perspective, it is important to look for explanations for not only why there exist vertebrates with lungs, vertebrates without lungs, and invertebrates without lungs, but also why there are no invertebrates with lungs. In *The possible and the actual*, Jacob (1982) points attention to the importance of constructing theories that correctly predict the actual (what is observed), but also ruling out what is logically possible but is not permitted by the system. Let us take a closer look at this distinction.

Suppose we have four traits, each of which has two trait values. Let us represent the dominant value with upper case letters, and recessive values with lower case letters:

A / a B / b C / c D / d

Suppose we find the following trait value combinations in our observations:

ABCD aBCD AbCD ABcD ABCd ABcd
AbCd Abcd

The following combinations are unattested (never observed) (*indicates what is prohibited).

*abcd *Abcd *aBcd *abCd *abcD

The constraint as formulated below would correctly account for the above asymmetry:

In every combination of (these four) traits, at least two of the trait values must be dominant.

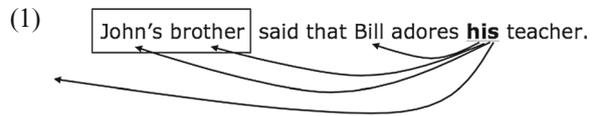
This defines what is invariant. Suppose it also turns out that combinations with the recessive trait value b are extremely rare. This can be expressed as a probabilistic constraint.

The probability of the occurrence of the recessive b is very low.

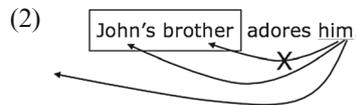
It might turn out that some of these constraints at a higher level are determined by the processes and constraints at the lower level, and in some cases, they are shaped but not determined. Such questions of predictability can be investigated only after the theory explicitly articulates the constraints.

Parallels of such structural constraints are common in the structure of human languages. In seeking to explain both persistence and change by constructing a biologically grounded theory of the human language faculty, linguists explain what is invariant (immune to change), what is recurrent (resists change but is still subject to it), what is variable (undergoes change freely), and the range of variability.

To take an example, consider the behaviour of pronouns in human languages. These are expressions like he, she, and they in English, and their translation equivalents in other languages, like *voh* (he/she/it) and *ve* (they) in hindi; *awan* (he), *awaL* (she) and *awar* (they) in malayalam, and so on. Pronouns have the property that they refer to some ‘antecedent’, either within the same sentence, someone mentioned in an earlier context, or someone pointed to.



If we were to ask a speaker of English (an experimental subject), whose teacher the sentence in (1) is talking about, she would say that it could be a teacher of Bill, or of John’s brother, or of John, or of someone not mentioned in the sentence (this is what the arrows in the picture indicate). Yet, in sentence (2), the pronoun him can refer only to John, or to someone not mentioned in the sentence. It cannot refer to John’s brother.



Why is this interpretation prohibited? The prohibition follows from a universal syntactic constraint called ‘disjoint reference’, whose effect can be paraphrased in ordinary English (without technical language) as (3):

- (3) If a pronoun is an object of a verb, it cannot refer to the subject or another object of the same verb (if the pronoun is a subject, it cannot refer to the object of the verb either).

This constraint holds on every human language investigated so far, without exception.

It must be noted that the term ‘constraint’ in the sense we are using it is simply a statement of an observed regularity (observational constraint, as in the case of Galileo’s laws) or a regularity postulated in our theory to explain an observed regularity (theoretical constraint, as in the case of Newton’s laws). They may also be higher theoretical regularities that explain lower level theoretical regularities.

Constraints in linguistics can also be language-specific in the sense that they apply only to a given language or language group. To illustrate, consider pronouns in Hindi. They observe disjoint reference. But in addition, they also observe a language-specific constraint called Subject Obviation, illustrated in (4):

(4) *raam-ke bhaai-ne arjun-ko uske ghar-me gaanaa sikhaayaa.*

Ram's brother Arjun his house-in music taught
Ram's brother taught Arjun music in his house.

In this sentence, the pronoun *uske* 'his' can refer to Arjun (the object of the verb), to Ram (the possessive in the subject) or to someone not mentioned in the sentence. But 'his' cannot be interpreted as referring to the 'subject', *raam-kaa bhaai* (Ram's brother). In nontechnical language, the subject obviation constraint can be stated as:

(5) If a pronoun and a subject occur in the same minimal clause, the pronoun cannot refer to the subject.

While this constraint applies to Hindi and many of the Indo-Aryan languages, it does not apply to English, the Dravidian languages, Chinese languages, and so on. In (6) below, for instance, the expression 'his house' can be interpreted not only as Arjun's house, Ram's house, or someone else's house, but also as Ram's brother's house:

(6) Ram's brother taught Arjun music in his house.

It is clear that there exist local (taxa-specific) constraints in biology. But are there universal constraints that apply to all taxa? This is the question we address in the next section.

Persistence, repair, and constrained randomness of mutation: Smith *et al.* (1985) carries an extensive discussion of the role of both local and universal developmental constraints on the trajectory of evolution, as distinct from the role of natural selection. They point out that Spurway (1949) adopts Vavilov's view (Vavilov 1922) that a species is a system that has its own potential for variation, and concludes that speciation modifies 'not only the anatomy and physiology of a species, but also its evolutionary future' (Spurway 1949, pp. 7). Extending this idea further, we may say that each taxon unfolds its unique potential for variation, and hence the evolutionary future for its descendants.

Now, what we see here is the idea that each node in a phylogenetic tree, ranging from the species node to the life node, is a system that constrains the evolutionary trajectory of its daughter nodes. A phylogenetic node in this conception can be viewed as a system of constraints. This idea can also be extended to the tree of traits and trait values. The two trees together yield Waddington's epigenetic landscape of evolutionary trajectories.

Coming to the physical mechanistic level, where are these constraints implemented? Given the research over

the past two decades on the role of repair mechanisms and their diversity, these repair mechanisms seem to be the most obvious candidate for implementing the constraints on evolutionary trajectories.

On what basis are the repairs effected? One may offer two speculations:

Conjecture 1: Errors of copying from the original are repaired.

Conjecture 2: Errors of copying where the outcome violates a constraint are repaired.

To illustrate the difference between the two conjectures, consider the possible errors in copying the English word *bit*. Each letter in this word can be replaced by 25 other letters. The possible errors are $25 \times 25 \times 25$. Under conjecture 1, the repairs are equiprobable. That is to say, the replacement of *b* by *p* to derive *pit* is as likely as the replacement of *i* by *p* to derive *bpt*. This is not the case under conjecture 2. A constraint on the structure of words in the written form in English is that *every word must have at least one vowel*. Under conjecture 2, the outputs *bpt*, *bkt*, *bft*, *bgt* and *bmt* will be repaired because they violate the constraint. But the forms *pot*, *set*, *bud*, *pam*, and *kid* are not repaired as they do not involve any violations.

Conjecture 1 is insensitive to structure. But conjecture 2 allows only for *structurally well-formed innovations*. This view of *structure preserving* repair mechanisms is consistent with the literature on repair. For instance, after a comprehensive survey of repair mechanisms, Aravind *et al.* (1999) conclude:

Comparative analysis of DNA repair systems, made possible by the availability of multiple complete genome sequences, suggests a remarkably complex picture of evolution, contingent on the external and internal environment and replete with domain shuffling, horizontal gene transfer, and lineage-specific gene loss events. Repair systems rely on a limited set of conserved domains but the number of universal repair proteins with domain architectures that are at least partially conserved across the three domains of life is very small, and there is no orthology at the level of systems and pathways. By contrast, a much greater level of conservation is observed within each of the three super kingdoms of life.'

The mutation itself (copying error) may be random, but the repair (correcting the copying error) makes it nonrandom. Thus, the relation between the original and the output of repair is not one of pure randomness, but of constrained randomness. And the constraints themselves grow in number as we move down from the root node to the terminal nodes in the phylogenetic tree of life. This view of constraints and structure preservation is in perfect harmony

with the core ideas of persistence discussed by Darwin, Vavilov, Waddington, Jacob, Spurway, and Smith and others, mentioned in the previous sections.

Structural constraints: Consider the following constraints on biological structure:

- All living organisms have cells.
- All living organisms have cell membranes.
- All living organisms have DNA, RNA, and protein.

These are universal structural constraints (note that under this formulation, viruses are not living organisms). A subset of these constraints is of the form, 'If P, then Q'. Take, for instance, the earlier constraint that if an organism has a beak, it also has feathers; or that if an organism has compound eyes, it also has six legs. These phenotypic correlational constraints are universal. Obviously, their genotypic equivalents will also be universal. It is important to study these universal constraints because they shed light on the genotype–phenotype correspondences in biology.

As pointed out in [Smith *et al.* \(1985\)](#), there are also taxa-specific structural constraints. Take, for instance, the phenotypic constraint that every organism must have cells with a cell nucleus. This constraint does not apply to prokaryotic cells; it applies only to the eukaryotic taxon. The constraint did not exist prior to the onset of the eukaryotic period, and evolved only subsequently. Likewise, the constraint that every organism must have a food tube came to exist along with the onset of the animal period, and applies only to the taxon of animals. An important point emerging from this discussion is that biological constraints themselves evolve.

Functional constraints: While some traits in biology are structural (e.g., wings, number of legs, beaks, lungs, vertebrae), others are functional–behavioural (e.g., flight, reproduction, respiration, territorialism). Thus it should not be surprising that in addition to the structural constraints discussed so far, constraints can also be functional. This opens up the possibility of some functional constraints being universal.

As a starting point for the formulation of universal functional constraints, consider the following candidates. All organisms have one or more systems to perform these functions:

- (i) *Structure building, maintenance and repair:* To create internal structure using matter and energy gathered from the environment (food serves to build cells, tissues, and organs); to maintain these structures during adulthood (cells are continually replaced in multicellular organisms); and to repair damage (mechanisms that repair a cut on the human skin).
- (ii) *Complexity increasing:* [Schrödinger \(1944\)](#) pointed out that, in contrast to Newtonian systems that are

order preserving, and thermodynamic systems that are order decreasing, biological systems are open systems that increase internal order or complexity. Biology exhibits two dimensions of increase in complexity; in both dimensions, the increase results in organizations consisting of multiple structures, systems, and functions:

- i) Development: a unicellular zygote develops into a multicellular organism.
- ii) Evolution: a prokaryotic population of organisms evolves into multiple cell types and multicellular organisms.
- (iii) *Input and output:* To take in matter and energy from the environment, process it internally, and expel waste matter (food–digestion–excretion).
- (iv) *Internal transportation:* To transport material from one part of the organism to another.
- (v) *Stimulus–response:* This makes living organisms cybernetic systems, with the following subfunctions:
 - (a) Sensory: to receive information from outside through organs/organelles;
 - (b) Cognitive: to interpret that information;
 - (c) Response: based on that interpretation, to respond to the environment either internally or externally (plants organize their leaves to receive maximum sunlight; bacteria move away from toxins and towards nutrients); and
 - (d) Learning: to learn from (i)–(iii), such that responses to the same stimuli after learning are distinct from those before learning. All living organisms are learning systems.
- (vi) *Internal coordination:* To coordinate diverse internal and external processes (the extraordinary coordination that human vision needs for hitting a moving tennis ball).
- (vii) *Internal cohesion:* To put parts together into a cohesive whole (the function of a boundary to demarcate the inside from the outside, e.g., cell membrane in unicellular organisms, skin in animals; or the 'us-and-them' function of immune cells).
- (viii) *Transmission:* To allow for vertical transmission of traits to the next generation (reproduction), and in many instances, horizontal transmission across peers within the same generation, or oblique transmission to an individual from non-parent members of the parent generation.
- (ix) *Communication:* Communication between different systems and structures internal to an organism, or between organisms (e.g. quorum sensing in bacteria).
- (x) *Defence:* Immune system.

The functional traits identified above are universal in biological organization. However, in their implementational details at the level of mechanisms, they are taxa-specific.

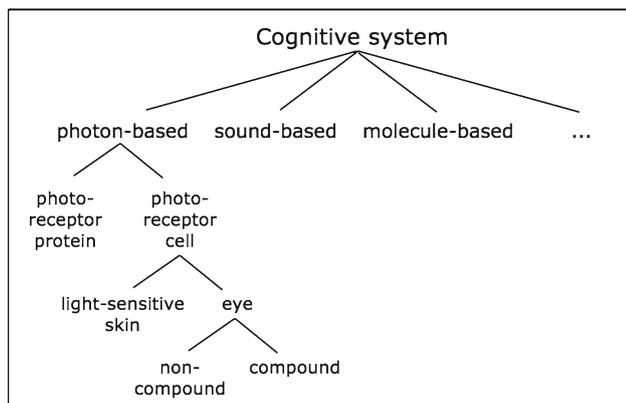


Figure 2. A tree structure of trait complexes that may be obtained from the study of the evolutionary history of cognition.

For instance, take the cognitive function that interprets the world. Shettleworth (1998, pp. 5) defines cognition as ‘the mechanisms by which animals acquire, process, store, and act on information from the environment. These include perception, learning, memory, and decision making’. Taking this definition of cognition, Lyon (2015) makes a persuasive case of bacteria possessing a molecular ‘tool-kit’ for sensing/perception, valence, behaviour, memory, learning, anticipation, decision making and communication.

Clearly, at the structural level, bacterial cognition is quite different from that of humans: human sense organs, for instance, include eyes, ears, nose, tongue, skin and muscles. Bacterial sense organs are the proteins on the cell membrane. Yet, cognition per se appears in both. And the universality of the cognitive function holds equally on plants. As Brenner *et al.* (2006) show, plants share with humans, the core characteristics of their cognitive system at the functional level and even at the level of implementation, to the extent that they call it the ‘neurobiology of plants’.

The recognition of such functional unity across taxa has an important consequence for the study of evolution. If we study the evolutionary history of cognition from prokaryotes to humans, we have a rich lineage of trait complexes that can be represented as a tree structure, along the lines of the rudimentary sketch below (figure 2).

Most of such universal functions and their taxa-specific implementation can be extended to cultural organization. Table 1 provides a few brief examples.

It would be valuable to look for such structural-implicational and functional-behavioural universals in the design of a unified theory of biological and cultural evolution.

Predicting the degree of persistence: We have seen that traits differ in their strength of persistence, and that the degree of persistence correlates with the hierarchical level of the

taxa in the phylogenetic tree: traits of higher-level taxa are more likely to persist.

The hierarchical organization of the function–system–structure of traits illustrated in the previous section yields a parallel way of understanding persistence. Given such hierarchical organization, we can see the correlation between the higher and lower nodes of the tree on the one hand, and the degree of persistence in evolution on the other. Clearly, the universal functions specified as A–J in the previous section, which constitute the root nodes of each trait tree, are protected from mutation in all taxa: they are maximally persistent. The existence of the eye as a mid-level trait is also preserved within higher animals. What can be subject to mutation are such things as eye colour, which is low in the hierarchy. We can now state a law governing persistence of traits as follows:

The persistence of a trait value is directly proportional to its distance from the root node of the function–system–structure tree.

The distance in this case is measured in terms of the number of intervening nodes, rather than the duration of time for evolution.

Concluding remarks

We began this article with the idea that the transdisciplinary concept of evolution—one that cuts across the physical, biological and human sciences—is best viewed in terms of symmetry breaking. We have suggested that evolution as symmetry breaking is a process that results in increased organizational complexity.

Viewed this way, we can reconceptualize symmetry breaking in biological evolution as the emergence and persistence of structures, systems, and functions. This translates as the emergence and persistence of novel distinctions in history, where history is defined as a sequence of changes from the past to the present.

We defined the concept of evolution as *the history of the emergence of diversity (novel distinctions), the persistence of the emergent, and increased complexity of organization*. This definition led us to an important question on evolution: *how do we explain the combination of change on the one hand and resistance to change on the other?* The answer that emerged as a response to this question is in terms of structural and functional constraints, whose strengths correlate with their position in the hierarchical structure of phylogenetic and trait trees. We have suggested that these universal and taxa-specific constraints are implemented at the molecular level in terms of repair mechanisms.

The trait-based approach to evolution, unlike the species-based approach, can be extended to cultural evolution. This expanded view yields a theoretical perspective that leads to questions about the evolution of the respiratory system, of visual perception, of economy, and so on, going beyond the focus on speciation and the phylogenetic tree.

Table 1. Extension of functions from biology to human culture and society.

Function	Biology	Human culture and society
Internal cohesion: boundary	Nuclear membrane; cell membrane; skin	National boundaries, with passport and visa requirements; fences; walls
Internal cohesion: 'us-and-them'	Immune cells	Nationalism, religious and ethnic groups
Defense	Immune system	The armed forces (army, navy, air force)

Acknowledgements

More than three years ago, Amitabh Joshi made a casual remark that my questions on biological classification and evolutionary theory led him to conclude that I was a Russelian. This remark puzzled me, as I view Russell as a formalist, and do not regard myself as one, even though I do take formalism seriously. While writing this article, I think I understood what he meant, and thank him for revealing to me what I am driven to pursue. I am also grateful to the members of the Foundations of Biology group for the various discussions and feedback.

Appendix

- Point 1. Einstein and Infeld's *Evolution of physics* (1938) is about the evolution of the conceptual foundations of theoretical physics, while Elliot Sober's *Reconstructing the past* (1991) and *Conceptual issues in evolutionary biology* (2006) are about the conceptual foundations of evolutionary biology.
- Point 2. Take, for instance, the distinction between the history of physics and the evolution of physics. When Einstein and Infeld wrote the book *Evolution of physics* in 1930's, they were concerned only with those aspects of the history of physics that contributed to its evolution.
- Point 3. 'Trait' is synonymous with 'parameter', 'factor', 'feature', 'attribute', and 'dimension', and 'trait value' with 'feature value', 'attribute value', 'allele', and so on.
- Point 4. A note on terminology: The concept of structure as used here is the same as 'organization' for Waddington, who says '... an entity can be divided into parts in innumerable different ways. We might use the word 'organisation' to refer to the relation between the whole and the parts, when the latter were derived in any way at all' (Waddington 1957). We use the term 'organization' to denote a complex of structure, system, and function. We may also note that it is distinct from the concept denoted by the word 'structure' in protein structure, where 'structure' denotes or at least includes shape. In protein structure, the term refers to what Aristotle called 'form'.
- Point 5. It must be made clear that the term 'law' or 'constraint' in the sense used here is not restricted to quantitative laws expressed in terms of statistics or calculus. Laws can be nonquantitative, expressed in terms of discrete mathematics or formal logic, as in the case the laws governing the structure of human languages or the organization of the language faculty of the human species.

References

- Aravind L., Walker D. R. and Koonin E. V. 1999 Conserved domains in DNA repair proteins and evolution of repair systems. *Nucleic Acids Res.* **27**, 1223–1242.
- Bhullar B.-A. S., Morris Z. S., Sefton E. M., Tok A., Tokita M., Namkoong B. *et al.* 2015 A molecular mechanism for the origin of a key evolutionary innovation, the bird beak and palate, revealed by an integrative approach to major transitions in vertebrate history. *Evolution* **69**, 1665–1677.
- Brenner E. D., Stahlberg R., Mancuso S., Vivanco J., Baluška F. and Van Volkenburgh E. 2006 Plant neurobiology: an integrated view of plant signaling. *Trends Plant Sci.* **11**, 413–419.
- Greenwold M. J., Bao W., Jarvis E. D., Hu H., Li C., Gilbert M. T. *et al.* 2014 Dynamic evolution of the alpha (α) and beta (β) keratins has accompanied integument diversification and the adaptation of birds into novel lifestyles. *BMC Evol. Biol.* **14**, 249 (<http://www.sciencemag.org/news/2015/05/how-birds-got-their-beaks>).
- Jacob F. 1977 Evolution and tinkering. *Science* **196**, 1161–1166.
- Jacob F. 1982 *The possible and the actual*. The University of Washington Press, Washington, USA.
- Lyon P. 2015 The cognitive cell: bacterial behavior reconsidered. *Front. Microbiol.* **6**, 264.
- Pennisi E. 2015 How birds got their beaks. *Science* **348**, 744.
- Racine V. 2014 Evolution and tinkering (1977), by Francois Jacob. *Embryo Project Encyclopedia* (<https://embryo.asu.edu/pages/evolution-and-tinkering-1977-francois-jacob>).
- Schrödinger E. 1944 *What is Life?* Cambridge University Press, Cambridge, UK.
- Shettleworth S. J. 1998 *Cognition, evolution, and behaviour*. Oxford University Press, Oxford, UK.
- Smith M. J., Burian R., Kauffman S., Alberch P., Campbell J., Goodwin B. *et al.* 1985 Developmental constraints and evolution: a perspective from the mountain lake conference on development and evolution. *Quart. Rev. Biol.* **60**, 265–287.
- Sober E. 1991 *Reconstructing the past: parsimony, evolution and inference*. Bradford Books: The MIT Press, Cambridge, USA.
- Spurway H. 1949 Remarks on Vavilov's law of homologous variation. *Ric. Sci.* **19**, suppl. 3–9.

- Thompson D. 1942 *On growth of form*. Cambridge University Press, Cambridge, UK.
- Vargas A. O., Kohlsdorf T., Fallon J. F., VandenBrooks J. and Wagner G. P. 2008 The evolution of HoxD-11 expression in the bird wing: insights from alligator mississippiensis. *PLoS One* **3**, e3325.
- Vavilov N. 1922 The law of homologous series in variation. *J. Genet.* **12**, 67–87.
- Waddington C. H. 1957 *The strategy of the genes; a discussion of some aspects of theoretical biology*. Allen & Unwin, London, UK.
- Waddington C. H. 1968 Towards a theoretical biology. *Nature* **218**, 525–527.

Corresponding editor: T. N. C. VIDYA