



The Comparative Method in Biology and the Essentialist Trap

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The comparative method is at the center of a complex view of biology, according to which organisms are seen as historical products. This is a dynamic view of nature, where genotypes and phenotypes change over evolutionary time under the influence of natural selection. Organisms (species) and groups of them (clades) are defined by their uniqueness, and their comparison provides insight into patterns of diversification. The alternative, mechanistic approach is enormously powerful, and has led to our understanding of basic molecular mechanisms underlying biological processes. However, because of intrinsic practical difficulties, this latter approach has only been applied to a very small cohort of animal systems, the so-called “model systems.” While this approach has been enormously productive, it has brought with it as a by-product a narrow view of biological diversity; and the assumption that with just a handful of well-studied animals we “understand” development and evolution. Nothing could be further from the truth, as indicated by many recent studies, which have shown that the development of animals is highly plastic. The lack of appreciation of this simple fact has brought me (and others) to see the field of developmental biology as caught within an “essentialist trap” from which many contemporary evo-devo approaches try to free it.

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INTRODUCTION

We make sense of the world around us by imposing order on it. One mental device we commonly use for this is identification of patterns or regularities. Patterns allow us to organize our knowledge, and provide us with tools for further interpretation of sensory and reflective information.

Sciences have always used raw, observable data to infer patterns, over space and time. These patterns have been used to generate hypotheses (falsifiable, *sensu* Popper, 2005) that allow us to understand, and predict, the workings of our physical world (and some of our internal mental states).

From the observation of stellar and planetary objects to the distribution of organisms within space and time, theories regarding the workings of the universe have relied fundamentally on the understanding and interpretation of patterns.

We recognize patterns in nature through a process that involves comparison: between the objects of the system analyzed and with those we infer to be outside references. This highlights the fundamental and primary use (and need) of the comparative method to understand the workings of nature.

Patterns suggest underlying mechanisms. As patterns are transformed into mental hypotheses, they thus have predictive value.

In nature, as Darwin understood early on, patterns of organismal diversity suggest a mechanism for the diversification of species. The appreciation that the fossil record also follows a very specific pattern (and is not a random distribution, between strata or across different geographical areas) reinforced the idea that organisms/clades diversified from ancestral stocks in a very precise way. The exquisite adaptation of organisms to their environment (a clear demonstration of how patterns can lead to clear inferences) suggested the theory of natural selection to Darwin and Wallace. Organisms/phenotypes and environments seemed to “fit” together perfectly well.

Processes (such as development) can be interrogated through external intervention (manipulation of the system); but not so patterns: patterns are mental (re) constructions. Process analysis gives us information on proximal causes while patterns inform us of ultimate (evolutionary) causes/mechanisms. Hence, understanding of natural diversity can be derived from a reconstruction of historical patterns or by the direct analysis of individual developmental trajectories.

These approaches are not mutually exclusive and clearly one cannot be classified as superior or inferior to the other. However, it is a sociological truth that we tend to think that the analysis of the mechanistic particularities of any biological process somehow represents a superior form of analysis; but this only reflects a particular (cultural) bias in our view of what it means to understand nature. This is merely the result of imposing our very personal (human, social, and political) “values” on research programmes, nothing else. Obviously, imposing values has clear ideological undertones (“this is more important than that”) and ultimately simplifies our view of nature to safeguard a particular cultural or political agenda.

Going back to my original assertion, nowadays we adopt two approaches to developmental biology: the mechanistic approach and the comparative approach. Let us revisit the historical origins of these views, before analyzing the consequences of practicing them for our perspective on this field. Needless to say, I understand that at different times both approaches have incorporated views that could be ascribed to the other approach, and thus we cannot consider them to be mutually exclusive.

THE CURRENTLY “FAVORED” MECHANISTIC APPROACH

The mechanistic approach focuses its attention, as its name indicates, on the “mechanics” of development, with all the different physicochemical contributions (mechanical, molecular, etc.). Its origin is linked to the stimulus provided by the notion of “Entwicklungsmechanik” or developmental mechanics (Gilbert, 1994). The growth of disciplines such as physiology and genetics (Dobzhansky, 1970), principally at the beginning of the twentieth century (plus the rise of molecular biology from the 1950s on), has provided biology with the opportunity to thoroughly characterize the mechanistic basis of biological processes, such as those underlying the development of organisms. The development of genetic manipulation techniques in the 1900s and genetic engineering in the 1970s and 1980s revolutionized

the study of molecular processes. The analysis of mutants and the identification of affected genes (plus the analysis of epistatic relationships, etc.) provided the Developmental Biology field the possibility of deciphering all the minute details involved in the generation of every single body structure, from the workings of individual cells to the generation of three-dimensional patterns (Davidson, 1987).

This possibility of dissecting processes in great detail has led to an overenthusiastic embrace of the mechanistic approach in developmental biology, to the detriment of the comparative/historical approach. It is not that the field lacks good reasons for this enthusiasm, but it is necessary to point out that it has brought with it the simplistic assumption that only mechanisms matter. Needless to say, a by-product of the insistence on the importance of (only?) understanding mechanistic aspects was the need to introduce a series of laboratory “models.” Those models were not selected at random; in fact, most of them are models that are very well-adapted to the needs of a laboratory system: easy to manipulate, with short intergenerational periods and robust against the vagaries of laboratory life or because the availability of different tools, such as genomes or lineage maps (Bolker, 1995, 2014). This selecting of “model” organisms could be justified by, mostly, one fact: basic cellular processes are common to all animals so the use of models can provide a general overall understanding of physiology. However, at the same time, the use of (a few) models has led to a narrow view of the processes that occur at a higher level (supra-cellular) in animals, since these processes tend to be quite diverse and thus cannot be well-represented by the idiosyncrasies of any specific animal model. (This sometimes even applies to those animals with clear phylogenetic affinities to the models: i.e., gene content, early cleavage, segmental patterning, etc.) In fact, the use of inbred lines of laboratory “models,” while particularly useful (reducing the degree of polymorphism that the researcher has to deal with) has produced a streamlined version of the animal species: a version that incorporates in its interpretation as a model clear essentialist/typological undertones (somehow reproducing Aristotle’s old idea of “Natural State Model”; see Sober, 1980). This latter aspect of the selection of “models,” and the narrow assumption of their being representatives of large clades, is what brought us (the field of developmental biology) to our current predicament; what I call an “essentialist trap” (more in later sections).

THE COMPARATIVE METHOD IN MORPHOLOGY

There is a long tradition in biology of using the comparative method to understand commonalities among animals (or collections of them: clades). Areas such as physiology, zoology, botany, paleontology, etc. have all benefited greatly from the study of regularities. The comparative method has led to our understanding of the underlying pattern “generator,” which is evolutionary history itself.

The use of the comparative approach dates back to Aristotle (and probably before) and this long tradition had a particularly

powerful impact on the French school of comparative anatomy in the nineteenth century (Geoffroy and Cuvier; see Russell, 1916), which through comparative anatomical studies provided a starting point for later considerations regarding the evolution (transformation) of animal morphologies (von Baer, Haeckel, etc.; see also Russell, 1916). The incorporation of a historical narrative (evolution) brought us the important concept of homology: shared characters derived from an ancestral form (Hall, 2001). Later on, and through a complex interaction with other disciplines such as molecular biology and phylogenetics, it was incorporated into the explanatory framework that we know today as Evolutionary Developmental Biology (EvoDevo) (Laubichler and Maienschein, 2007; Wagner, 2014). The importance of morphology is key to our current understanding of the origin of biodiversity on Earth. The thorough characterization of patterns of diversification, and their underlying mechanisms, can be inferred only in relationship to historical changes of morphological and also molecular characters. Selection, adaptation, drift and constraints, are all concepts that are used regularly in biology and that are eventually substantiated in nature through variations in morphological characters. It is true that molecular characters are also relevant, but it is through variations in morphology that we appreciate the enormous diversity of life.

TAXONOMY AND THE COMPARATIVE METHOD IN PHYLOGENETICS

According to a common definition (Encyclopaedia Britannica): Taxonomy is “the science of classification, but more strictly the classification of living and extinct organisms—i.e., biological classification. In this sense understanding the taxonomic arrangement of our study models, and the clades to which they belong, offers a unique view at the variability and significance of any analysis of character evolution (a key issue in EvoDevo).

The story of taxonomy is a long one, originating a few millennia ago for utilitarian reasons (i.e., pharmacopeias). However, we had to wait until Linnaeus, who recognized the foundational nature of classification, for the introduction of the well-known binomial system. Nowadays, and following in the tradition of Linnaeus, we classify animals based on their phylogenetic (historical) affinities. However, it is through the important work of Willi Hennig’s that phylogenetic systematics became the basis for a phylogenetic view of taxonomy. His introduction of the crucial idea of contrasting plesiomorphic with synapomorphic and autapomorphic characters, plus the realization that synapomorphies could identify sister groups, provided the grounds for a new, evolution based, classificatory schemes.

Since the very nature of Taxonomy is comparative it is still surprising that a certain essentialist view of clades also permeates some phylogenetic analysis (perhaps haunted by Aristotle’s “Natural State Model”), with single species or individuals taken as proxies for the whole clade. The result of these choices can bias our interpretation of relationships, which sometimes has an impact on our interpretation of “ancestors/ancestral states.” In

this context, the introduction of a wider set of representatives per clade should give us a more accurate view of relationships (and also prevent us falling into the trap of the “representative model” Bolker, 2014). This consideration applies to both living and fossil representatives. Since many authors have stressed this need for increased taxonomic sampling, I will not dwell on the subject any further (see, for instance: Hillis, 1998).

THE COMPARATIVE METHOD IN EVOLUTIONARY DEVELOPMENTAL BIOLOGY (EVODEVO)

Animals are the products of their evolutionary history, and as such every single individual is the unique result of a complex interaction of genomes and environments over evolutionary time. Arguably, the origin (and the expansion) of the discipline of EvoDevo, which originated after the “modern evolutionary synthesis” context (when the study of development was also incorporated as a necessary aspect; what some authors call the “extended evolutionary synthesis”) was a response to the need for an understanding of the consequences of this enormous diversity of evolutionary trajectories (see, for instance: Laubichler and Maienschein, 2007). Not only did those aspects linked to the adaptation to the environment need to be understood, but so too did the basic mechanisms underlying the exquisite adaptation observed. From early on, the realization that development was plastic at all stages, from early embryogenesis to later aspects of morphogenesis, suggested that we should be careful not to overgeneralize the mechanisms of development. In this context, EvoDevo was born out of the need to highlight the ontological deficiencies of the “model system” approach; again, what I call the “essentialist trap.” We have discovered that changes in mechanisms can occur in (relatively) short periods of evolutionary time. In fact, even drastic changes in the early development of embryos (from indirect to direct developmental modes; see Smith et al., 2007) can happen in just a few million years. Moreover, changes in the morphology of adults (and the underlying genomic sequences) also happen in shorter periods of time, as adaptations to continuously changing environments (for instance, the paradigmatic “Darwin’s finches” Grant and Grant, 1994). These conspicuously present changes in species point to a characteristic aspect of development, its plasticity, and thus bring us to the idea that patterns and the underlying mechanisms do not have to be “locked out” for long periods of evolutionary time. This means that there is no specific reason to believe that model systems are representative of large swaths of universal developmental processes, encompassing large groups of animals (clades). EvoDevo should keep an eye focused on variation, and variability can only be understood through the use of comparative methods.

I think it needs to be emphasized (to avoid the “reverse” biased position), and before finishing this section, that the so-called model systems have been particularly useful as references to understand the evolution of close-related species or clades. Several cases come to mind, for instance the use of *Drosophila melanogaster* to illuminate the variability in the developmental

aspects of segmentation in arthropods (Averof and Akam, 1993 or the recent synthesis: Minelli, 2017), or the genetic co-option of regulatory genes in the formation of eyespots in butterflies (i.e., Brunetti et al., 2001); but also, the nematode *Caenorhabditis elegans*, instrumental in our current understanding of the plasticity of cell lineages given rise to the vulval structures (i.e., Sommer and Sternberg, 1996) or the zebrafish *Danio rerio* that has led to our current view of variation in the vertebrate gastrulation (i.e., Shih and Fraser, 1995).

A generalized problem with using “model systems” to draw conclusions about the evolution of development has been the careless jump to easy conclusions based on the comparison of models who have diverged over, sometimes, hundreds of millions of years. This was a problem accentuated a few decades ago when only mice and *Drosophila* were established models. These animals belong to clades that diverged more than 500 millions of years ago, in the Cambrian! (or before). Over such a huge evolutionary distances it is hard to make, most of the times, sensible comparisons. A few classical examples are illustrative (De Robertis and Sasai, 1996; Gehring, 1996).

WHY DO WE NEED MORE COMPARATIVE DATA? PATTERNS EMERGING

The comparative method saves us from the trap of “normalizing” developmental processes. This, as stated before, is a trap very closely linked to growing use of the “model organism” metaphor. Let us be clear about one thing: there is no such thing as a “model organism” in nature; so-called “model systems” do not even represent their congeners living in the wild. In this context, I would like to stress once more that the comparative approach suggests a much more interesting (richer) natural world, with developmental processes being subjected to variation in many different ways, responding to the contingences of the natural habitat and also limited by different historical constraints. Organisms are thus products of their evolutionary history and show the enormous variation resulting from their different adaptations.

Variations in development occur at many different levels, from the changes in early embryonic specification to changes in the underlying gene regulatory networks (Davidson and Peter, 2015). Final phenotypes reflect the fine adaptations to the minutiae of environments (plus the inescapable burdens of history; the exaptations, according to Gould and Vrba, 1982). Variations are obvious at many taxonomical levels, from the ground plan (or “Bauplan”) of phyla to the small variations present in the individuals of each species (including subspecies, plastic morphs, etc.). A full understanding of this intrinsic property of nature, “variability,” relies on the use of “population thinking” (Mayr, 1982) in the broadest sense of the term, including individuals and clades (as “kinds of biological objects”). This view should be widely adopted in Developmental Biology; otherwise we will be building a science of particularities not a science that interrogates and reveals “real” nature.

In the face of the enormous variety of morphologies (and their genomic and developmental underpinnings) it is hard to

understand the insistence on the concept, or the metaphor, of model organism. From the biological point of view, this view is misleading and ultimately wrong. Moreover, as I say above, the use of inbred lines as laboratory “models,” while they may have particularly useful properties (reducing the degree of polymorphism to be dealt with), has generated more streamlined versions of the animal species, thereby also contributing to the propagation of an essentialist/typological view of development.

I do not wish to leave the reader with the impression that model organisms are useless. Of course, understanding the complexities of nature might require some simplifications, but this should not blind us to the real fact that nature is enormously varied. Needless to say, there are obvious reasons for avoiding a “generalized” introduction of new model systems, whether for budgetary (Sommer, 2009) reasons or due to the specific interest in the biological problem analyzed (Jenner and Wills, 2007). It is certainly true that a clear focus on solving specific biological problems should be maintained, but not under the umbrella of the idea that models represent extensive swaths of organisms (clades) and developmental mechanisms.

An “essentialist” view of nature might be instrumentally useful in some cases, but nonetheless, it is generally flawed (Mayr, 1982 “The growth of biological thought”; see also Grene, 1990 for a critical view of Mayr’s contribution to this debate). The comparative method reveals a much richer and more accurate view of biological diversity. As perceptively put by Hallgrímsson and Hall (2005): “Understanding how variability arises from developmental systems requires approaches that focus on the patterns and nature of the interactions among elements in the system.” The analysis of variability is, in the long term, a richer source of information about developmental mechanisms than the limited (straightjacket) view provided by the study of so-called “model” organisms. Needless to say we shouldn’t forget that EvoDevo deals with genomes, cell types, and morphological characters of many types, hence, I also vindicate here a fuller view of the evolutionary history of organisms, one that incorporates analysis at many different levels.

To sum up, what I hope I have contributed to with this paper is a more balanced view of diversity, and hence the necessity for funding agencies to recognize the value of studying animals other than those considered to be “models.” Failing to accept this obvious fact is to delude ourselves: keeping ourselves prisoners of an “essentialist trap” for quite some time to come.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and approved it for publication.

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