

Typology and Natural Kinds in Evo-Devo

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Abstract

The traditional practice of establishing morphological types and investigating morphological organization has found new support from evolutionary developmental biology (evo-devo), especially with respect to the notion of body plans. Despite recurring claims that typology is at odds with evolutionary thinking, evo-devo offers mechanistic explanations of the evolutionary origin, transformation, and evolvability of morphological organization. In parallel, philosophers have developed non-essentialist conceptions of natural kinds that permit kinds to exhibit variation and undergo change. This not only facilitates a construal of species and higher taxa as natural kinds, but also broadens our perspective on the diversity of kinds found in biology. There are many different natural kinds relevant to the investigative and explanatory aims of evo-devo, including homologues and developmental modules.

Keywords

essentialism, evolvability, natural kinds, mechanistic explanation, morphological organization, variational structuralism

Introduction

Although typology and natural kinds are conceptually distinct issues, they have converged prominently in discussions of the nature of species and higher taxa. This is because natural kinds are traditionally deemed to be defined by essences, and critics of typology have opposed

essentialism about species, arguing that species and higher taxa are not natural kinds but individuals. However, more recently, skepticism about typology and natural kinds in evolutionary biology has subsided. Part of the reason derives from scientific developments. The use of such notions as body plan in evolutionary developmental biology (evo-devo) has made the idea of morphological type reputable again (or at least more reputable) by embedding it within the agenda of mechanistically accounting for the origin and subsequent evolvability of morphological organization. In a parallel trend, philosophers have advanced non-essentialist conceptions of natural kinds that can capture variation and evolutionary change. While these conceptions permit biologists to theorize species and higher taxa as natural kinds, the more general lesson emerging from these parallel developments is that there are a diversity of biological kinds beyond taxa relevant to the investigative and explanatory aims of evo-devo.

Typology and Body Plans

The establishment and investigation of types has been a central practice in comparative morphology, especially in the tradition of structuralism, which emphasizes form and structural commonalities across taxa independent of functional considerations (see the chapter on “Form and Function”). Although typology has a long and venerable history, it has been controversial ever since Ernst Mayr (1959) contrasted ‘*typological thinking*’ with ‘population thinking.’ Mayr objected to characterizing a species by means of a set of typical traits, for example, using particular plumage features and vocal traits to characterize a bird species such as *Elaenia obscura* as a whole. Instead, he argued that species should be conceived in terms of variation across individuals, which is subject to the operation of natural selection. He credited Darwin with having introduced population thinking, according to which the (statistically characterized) traits

of entire species are derived exclusively from the traits of individuals. As a consequence, species traits are subject to constant change. Mayr acknowledged that some morphologists who invoked types did accept evolution, but he objected that only saltational evolution is possible from the perspective of typological thinking, whereas gradual evolution was ruled out by definition. Based on a similar criticism of traditional taxonomic methodology made by David Hull (1965), who dubbed the flawed approach ‘essentialism,’ typological thinking and essentialism often came to be viewed as synonymous labels for a misconceived (if not erroneous) way of reasoning about species, which fails to comport with Darwinian evolutionary theory (Amundson 2005; Winsor 2006).

Essentialism links directly to the topic of *natural kinds*. Traditionally, any species taxon was deemed to be a class, defined by some set of shared properties, or a natural kind, which philosophers often viewed as having an essence. It is certainly appropriate to construe chemical elements as natural kinds, where the specific atomic number can be seen as an essence shared by all elements of the same type (e.g., oxygen atoms). However, Michael Ghiselin (1974) and David Hull (1978) challenged the view that species are classes or kinds and introduced the now dominant species-as-individuals thesis. On this view, a species taxon is an individual, a complex whole that has organisms as its parts, very much like an organism is an individual composed of various cells. Any account of the ontological nature of species has to capture three features: (i) a species is denoted by a proper name, (ii) a species is a concrete thing that occupies a certain region of space and exists during a particular period of time, and (iii) a species exhibits variation at any point in time and can undergo change across time. Ghiselin and Hull argued that abstract classes (or kinds) fail to capture these features. However, the notion of an individual appears to capture all three. Given within-species variation and evolutionary change, neither a phenotypic nor a genotypic trait could be the essence of a species construed as a natural kind. The

individuality thesis, in contrast, is not committed to shared traits. In fact, the parts of any complex individual can be quite different, just as different cells that compose an organism can belong to different cell types.

In his detailed discussion of the historical roots of evo-devo, Ron Amundson (2005) addresses how Mayr and other neo-Darwinians promoted the ‘essentialism story’ as both an historical account of previous biological traditions (with a special emphasis on their flaws), and also used it as a tool to criticize contemporary approaches. This account has been shown to be historically inaccurate. For example, although there were species fixists before Darwin, these biologists did not appeal to species possessing essences as the explanation of fixism. More important for the issue of typology, Amundson notes that whereas neo-Darwinian objections to reasoning in terms of types pertain to species, previous comparative morphologists never invoked species types; instead, morphological types were formulated for *higher* taxa. And, just like structuralist morphological investigation in general, the notion of the *unity of type* pertained to relations across various species. This was already present in the period before Darwin, such as within the tradition of transcendental morphology (see the chapter on “Transcendental Morphology”) in Germany and Geoffroy St. Hilaire in France, and continued with subsequent traditions, some of which conducted morphological investigation and explanation explicitly within an evolutionary framework (Hall 1999; Russell 1982[1916]). Notably, soon after Darwin proposed his theory, the evolutionary morphology (see the chapter on “Evolutionary Morphology”) of Gegenbaur and Haeckel used comparative anatomical and embryological studies to establish relationships among taxa in the form of phylogenetic trees. Moreover, some conceptions of morphological types were not simply abstract descriptions of anatomical traits, but also could be invoked to explain why some structural pattern is present within a taxon or why some structural transitions between taxa are possible (and others impossible). For example,

mammals do (and must) have fewer jawbones than birds because they have more ear ossicles, which are homologous to avian jawbones (Amundson 2005). Although the vertebrate archetype advanced by Richard Owen in 1848 has been repeatedly (though inaccurately) portrayed as a Platonic type, Owen was quite open to historical transformations between species, albeit not by means of natural selection but by developmental forces guided within the explanatory framework of the archetype (Rupke 1993).

Earlier, upon its initial introduction in the 18th century, the Linnaean taxonomic system tended to be viewed as an arbitrary human convention. Yet the establishment of the idea of the unity of type in the first half of the 19th century fostered a different view—that the taxonomic system reflects relations, such as homologies, that really exist between species (Amundson 2005). This basic vision has been reinforced with the advent of modern phylogenetic systematics. Comparative studies in molecular and developmental biology have uncovered the phenomenon of ‘deep homology’: developmental genes and mechanisms are widely conserved across taxa, including animals, plants, and other eukaryotes (see the chapter on “Developmental Homology”). Contemporary accounts of *body plans* (see the chapter on “Body Plan | Bauplan”) contribute to the traditional idea of the unity of type by adding developmental processes and features to the structural traits shared by a taxon, e.g., the phylotypic stage of development (Hall 1999; Raff 1996; Slack et al. 1993). This evo-devo vision contrasts with what Amundson (2005) dubs the ‘residual conception of homology’ that is common among neo-Darwinians. A residual conception looks backward phylogenetically at homologies as nothing but traits that have not (yet) been modified by natural selection. From an evo-devo perspective, however, homologous developmental processes and overall body plans are governed by *developmental constraints* (see the chapter on “Developmental Constraints”), and thus have an important impact and shaping influence on future evolutionary trajectories.

In summary, although typology and the study of types has meant many different things in the complex history of comparative morphology, it is fair to say that current ideas of deep homology, developmental constraints, and body plans demonstrate that theorizing higher taxa in terms of shared developmental and morphological features is a reputable biological practice: “typology naturally emerged from the facts of evolutionary developmental biology and it would be seriously problematic to try to avoid it” (Wagner 2014: 5). Furthermore, neo-Darwinian criticisms of ‘typological thinking’ as leading to erroneous ways of thinking about the variation and evolution of species do not carry over to higher taxa. However, the tenet that natural kinds are not the appropriate ontological category for species because they undergo evolutionary change also has been invoked for higher taxa and homologues. Some argue that an evolutionary perspective mandates that each higher taxon and each homologue be conceptualized as an individual (Ereshefsky 2009; Grant and Kluge 2004; Jenner 2006). Therefore, we need to see more clearly how recent conceptions of natural kinds can capture variation and evolutionary change.

Conceptions of Natural Kinds Capturing Variation and Evolutionary Change

Although some biologists have recently endorsed the notion of natural kinds, it is an idea originally developed by philosophers. A kind is a grouping of several objects (the members of the kind). The key issue is to distinguish between kinds where the grouping conforms to reality—so-called *natural* kinds—and where the grouping merely reflects an arbitrary human convention—sometimes called *nominal* kinds (Khalidi 2013). Thus, a kind is a ‘natural’ kind not because its *members* are natural objects (as opposed to artefacts), but rather because the *grouping* corresponds to a division in nature (i.e., reality). The metaphor that a natural kind carves nature

at its joints is often used to express this basic idea. For traditional philosophical accounts, a natural kind is characterized by an *essence* (usually a microstructural property), which has two functions. First, the essence constitutes the kind's identity: an object is a member of this kind if and only if the object possesses the essential property. Second, the essence is causally basic: this property accounts for the presence of other properties characteristic of the kind. In this respect, the essence also fulfills an explanatory function. Something is an oxygen atom if and only if it has eight protons; moreover, the atomic number essence also accounts for or explains the various chemical properties common to oxygen atoms, such as the ability to form particular bonds and participate in certain chemical reactions.

In the last three decades, philosophers of science have developed new conceptions of natural kinds that relax the emphasis on essences and are deliberately meant to capture the kinds found in biology and other special sciences (Khalidi 2013; Magnus 2012; Wilson et al. 2007). These approaches do not assume that kinds have sharp boundaries or that they are governed by exceptionless generalizations (e.g., classical laws of nature), which would prevent members of the kind from varying among each other. The most influential of these newer approaches is Richard Boyd's (1999a) account of natural kinds as *homeostatic property clusters* (HPCs). A property cluster is any set of properties that exhibit correlations with one another. Correlations are usually not perfect, so that kind members need not possess each of these properties from the cluster. This allows for internal diversity and vague boundaries for kind membership, while at the same time corresponding to the fact that a simple correlation is sufficient for the purpose of prediction, generalization, or explanation in many scientific contexts. The property correlations of an HPC must be due to some underlying features of reality in order to qualify as a natural kind, as opposed to a nominal or conventional kind. Boyd calls these underlying features 'homeostatic mechanisms,' which, in contrast to a classical essence, need not be a single

property, but can consist in complex processes or assemblages of properties.

Importantly, the HPC kind account asserts explicitly that the properties defining a kind need not be intrinsic properties (e.g., internal structure or microstructure). Often the relevant properties are *relational* (Griffiths 1999). A good example of this situation is a higher taxon, which is defined in terms of descent from a particular ancestral species. An extant species possesses the property of ‘being descended from ancestor A’ not because of its intrinsic, internal features, but because of how it is (historically) related to another species in a lineage. Although this defines who is a member of the kind, the relational property of common ancestry permits variation in *other* properties, such as the genetic and phenotypic traits of different species within this higher taxon. Thus, an HPC conception of natural kinds in terms of clustered (yet imperfectly correlated) properties that includes relational properties can capture the variation exhibited by biological kinds synchronically (i.e., at one point in time) and diachronically (i.e., across time), including evolutionary change through phylogenetic history (Brigandt 2009; Wilson et al. 2007).

Using a naturalistic philosophical framework, Boyd (1999b) and many other contemporary philosophers of science base their account on actual scientific kinds and eschew any general theory of natural kinds put forward in a priori fashion. The same orientation holds for an account of the features of a particular kind (e.g., stem cells); the composition of the homeostatic property cluster characterizing a kind is always an empirical question. Conceptualizing species as HPC kinds is a good illustration of this approach even though species taxa motivated the claim that they are individuals and could not be natural kinds. There are a number of different species concepts that could result in species taxa with different boundaries. However, whatever underlying criteria are used to define a species taxon in a certain context, the HPC approach can

rely on them (Brigandt 2009). Interbreeding is one prominent way to define species. The property ‘being able to interbreed with’ is relational; an organism possesses it only in comparison to and interaction with other organisms. The homeostatic mechanisms underlying such an HPC kind therefore include a relation, which is an interaction that permits dynamic change in intrinsic properties (such as an organism’s genotype and phenotype). Thus, Boyd’s label ‘homeostatic’ should not be taken too literally—interbreeding and gene flow fully permit new variation and evolutionary change. The key point is that due to interbreeding a newly introduced genetic variant will spread within the species, resulting in some degree of species cohesion at any point in history, so as to make the kind natural rather than nominal.

The same situation obtains for other species criteria used by biologists, which can then serve as features characterizing a species taxon as an HPC kind. For instance, the ecological species concept focuses on members of a species occupying the same adaptive zone, which accounts for some degree of cohesion while permitting evolutionary change. Biologists and philosophers who maintain that species are not kinds but individuals have been largely silent on the features and mechanisms that underlie the cohesion and identity of a species. Yet proponents of the species-as-individuals thesis need to account for what makes certain organisms (but not others) count as parts of a species conceived of as an individual. (Ironically, in the history of philosophy, the ontological category of individual often has also been characterized by an essence, where an individual’s essence accounts for why the individual’s parts are not just a heap of objects but form a unified whole.) Foregoing a discussion of such features and mechanisms is more problematic scientifically than merely shying away from the ontological label ‘essence,’ as the next section details.

Kinds Answering to the Aims of Evo-Devo: Beyond Taxa

Following Richard Boyd’s seminal account of natural kinds as homeostatic property clusters, which departs from traditional, essentialist accounts, a number of philosophers have adopted and developed the view that species and higher taxa are HPC natural kinds, and a few biologists have followed suit (Assis 2011; Franz 2005; Rieppel 2005b, 2009; Wagner 2014), even though the individuality thesis remains the dominant position. Those taking a natural kind approach typically have assumed that species can be considered as both kinds and individuals (Boyd 1999a; Brigandt 2009; LaPorte 2004; Rieppel 2007b), which brings us to the broader issue of the epistemic role of natural kinds in science.

Regardless of whether several entities are viewed as members of a natural kind or as parts of a whole (for the individuality account), there are *epistemic* benefits to grouping entities together and representing their features (Boyd 1999a; Brigandt 2009). Shared features and property correlations can be used for the purpose of generalization and prediction (see the chapters on “Generalization” and “Prediction and Retrodiction”). Some of the features may be causal dispositions or stand in causal-dynamical relations to one other (e.g., the relational properties and homeostatic mechanisms acknowledged by the HPC account). As a consequence, they can be used for the purpose of scientific explanation (see the chapter on “Explanation”). A core motivation for the HPC account has been that natural kinds (in contrast to merely nominal or conventional kinds) are central to scientific inference, generalization, and explanation. Whether natural kinds play one or more of these roles depends on the particular kind at hand (e.g., whether it is primarily used for generalization or for explanation) and how concrete explanations are understood (e.g., as the description of a mechanism). In a similar attempt to move beyond the traditional ‘metaphysics of essentialism,’ Alan Love (2009) calls for an ‘epistemology of

representation.’ Scientific representations and typologies (e.g., normal stages of development) may abstract away from some features and variation found in nature, which is licit as long as this is conducive to the epistemic purpose at hand. Other representations or kind concepts are used in different contexts where the features originally abstracted away from are now scientifically relevant and therefore included.

In addition to representations of natural phenomena, such as the knowledge embodied in a kind concept, an important aspect of this epistemic dimension is what particular scientific *aims, needs, and purposes* a kind concept is to serve (Brigandt 2009; Reydon 2016). Natural kinds traditionally have been assumed to cut nature’s joints. However, whether something is a natural kind depends not only on metaphysical divisions in nature, but also on whether particular divisions are conducive to our epistemic agendas. As Jessica Bolker (2013: 126) puts it: “the relevance (or naturalness) of a concept depends on the epistemological context. What the term ‘natural’ in ‘natural kinds’ ought to describe is the fit between the classification scheme, and the work we want it to do.” The diversity of scientific aims—and the various needs of evo-devo in particular—is a motivation to consider kinds other than species and higher taxa.

A good case in point is developmental modules, which several biologists have described as natural kinds (Rieppel 2005a; Wagner 1996). Their significance for evo-devo lies in the phenomenon of modularity, which pertains to an organism’s organization both in terms of its component modules and the relations among those modules (see the chapters on “Modularity” and “Modularity in evo-devo”). While a module exhibits extensive internal developmental-causal connections (i.e., a form of integration), the developmental relations between modules are such that changes in one module need not significantly affect other modules (i.e., modules display relative autonomy), and one module can become developmentally linked to another

module it was not connected to before. Therefore, modularity in development enables the evolutionary transformation of organismal organization and the generation of morphological novelty. These questions comprise central explanatory aims of evo-devo's research agenda. Modules (as natural kinds) may be individuated based on developmental criteria, but the choice of suitable criteria in evo-devo should be made with an eye to the evolutionary potential of modules.

Another closely related issue is the treatment of characters and homologues as natural kinds. Evo-devo researchers can view an individual homologue as a unit of evolutionary transformation, where this evolutionary potential is due to the developmental organization and processes of organisms (Brigandt 2007; Rieppel 2007a; Wagner 2001). Although some have argued that a homologue—the overall transformation lineage consisting of a part of an ancestor and the corresponding parts in the descendants—can be construed only as an individual (Ereshefsky 2009; Grant and Kluge 2004), this is another instance where a non-essentialist conception of natural kinds can capture evolutionary change. In this case, developmental processes that account for a homologue being a sufficiently individualized organismal part form the mechanistic basis of an HPC kind that can undergo evolutionary transformation independently of other homologues. Amundson's (2005) notion of 'developmental types' (e.g., the vertebrate limb and its development) aligns with a natural kinds perspective on characters (Lewens 2009; Wagner 2014), while fruitfully highlighting that developmental types are hierarchically structured.

Günter Wagner (2014) uses the label '*variational structuralism*' for a modern form of typology that is enriched by evo-devo knowledge. It is explicitly dubbed 'variational' because it includes the generation of structural variation across individuals and species that results in

morphological evolution. As noted, some traditional approaches that endorsed typology certainly had evolution in view, but variational structuralism adds a mechanistic explanation of how morphological variation and transformation occurs developmentally to engender evolutionary change in morphological types. The research agenda is to understand the causal basis of *morphological organization*, including its hierarchical structure and developmental mechanisms. This then serves the aims of evo-devo biologists in explaining how morphological organization originates in evolution, how individual characters can vary and undergo evolutionary change (while the overall morphological organization of a taxon remains stable), and how morphological organization is transformed, such as by the addition of novel characters (Brigandt 2007; Wagner 2014; Wagner and Stadler 2003). Whether the focus is on an individual homologue (transformational character) or a body plan (organized, variational type), construing these as natural kinds yields kinds that exhibit *evolvability* (see the chapter on “Evolvability”). Accounting for evolvability is a core concern for evo-devo. Evolvability is a dispositional property—it is not about the variation already found within a population (on which neo-Darwinism focuses), but about the potential to generate phenotypic variation and novelty (see the chapter on “Epigenetic Innovation”). Given that evo-devo biologists are trying to understand how developmental potential facilitates morphological evolution, dispositional properties are common in evo-devo theorizing (see the chapter on “Dispositional Properties in evo-devo”). This is not in conflict with a natural kind perspective because many kinds are characterized by causal dispositions (even a traditional essence, e.g., a microstructural feature, can have causal capacities).

In addition to kinds that play roles in the investigation and explanation of evolutionary phenomena, natural kinds defined by purely developmental criteria also are of interest to evo-devo researchers (Nathan and Borghini 2014). Stems cells, even when restricted to those found

in a single species, must be construed as a kind that exhibits significant internal variation; a similar situation holds for genes (Reydon 2016; Slater 2013; Wilson et al. 2007). Although normal stages of development obscure evolutionarily significant within-species variation in development (and an evolutionary explanation of development must view stages as subject to transformation), standardized developmental stages provide an important reference point for explanations of a species' ontogeny (Bolker 2013; Love 2009). In general, different biological kinds may be individuated by quite different conditions, including causal features that enable transformation, causal features that maintain stability, and even non-causal criteria. This ontological diversity has led philosophers to argue that not all natural kinds found in biology are HPC kinds (Ereshefsky and Reydon 2015; Khalidi 2013).

Another ontological category of relevance to evo-devo is developmental processes. The general biological significance of processes within organisms (e.g., gene regulatory networks) and between organisms (e.g., ecological interactions involving multiple microbial species) has motivated some to call for a process ontology for biology (Baptiste and Dupré 2013). A process ontology views processes as a core ontological category, often with the claim that processes are more fundamental than structures. Processes are inherently dynamic. Indeed, even though the phenomenon of developmental robustness (which is likewise an investigative and explanatory concern of evo-devo) pertains to maintaining a certain phenotypic trait in ontogeny, this stability is often due to underlying dynamic processes that reconfigure a developmental system in the face of perturbations (see the chapter on "Robustness"). Processes are open-ended, without clear-cut boundaries (Rieppel 2009). This makes it difficult to individuate processes. Often epistemic considerations are used to make a contextual individuation choice (Brigandt 2017). Thus, there may be no principled way to count several processes as being of the same type or belonging to the same kind. Instead, only pragmatic considerations may suffice. More work is required to

understand the significance of an ontology of processes for illuminating the epistemology of evo-devo and other biological sciences. The complexity of biological phenomena makes it plausible that ontological categories beyond the notion of natural kinds will be necessary.

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Cross-References

Body Plan | Bauplan

Developmental Constraints

Developmental Homology

Dispositional Properties in evo-devo

Epigenetic Innovation

Explanation

Evolutionary Morphology

Evolvability

Form and Function

Generalization

Modularity

Modularity in evo-devo

Prediction and Retrodiction

Robustness

Transcendental Morphology

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