Chapter 23
Pattern and Process in Evo-Devo: Descriptions and Explanations

Laura Nuño de la Rosa and Arantza Etxeberria

23.1 Introduction

The dialectics between pattern and process is a main connecting thread in the history of natural history and modern biology. Ontology is organized differently according to pattern-based or process-based philosophical views: the former mainly considers structures, whereas the latter perceives reality as consisting of systems in a permanent state of change. As regards epistemology, patterns apply to the description of phenomena, whereas processes are associated with their explanation. Similarly, in evolutionary biology patterns or structures are usually the phenomena (*explanandum*) that come into being through processes (*explanans*). To be precise, *patterns* refer to hierarchies (e.g. cladograms) or temporal sequences (such as the paleontological ones), whereas the phylogenetic order is attributed to causal *processes* such as changes in gene frequencies resulting from genetic drift or natural selection (Grande and Rieppel 1994). In the Modern Synthesis, the distinction between patterns and processes had strong epistemological consequences: the study of *pattern* was ascribed to the *descriptive* fields (systematics, paleontology, comparative anatomy), whereas population genetics and evolutionary ecology were considered to be the *explanatory* disciplines responsible for studying the causal *processes* driving evolution (Arthur 2000).

However, the questioning of the Neo-Darwinist framework by morphological and developmental approaches may bring about a re-conceptualization of both pattern and process. In relation to *patterns*, phenomena such as biases in the variation of morphological traits, rapid changes of form in the fossil record or the evolutionary stability of morphological organization revealed by homologies and body plans (Müller 2006 and references therein) highlight the need to pay more attention to

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L. Nuño de la Rosa (✉)
Complutense University of Madrid, Madrid, Spain

IHPST, University of Paris 1 Panthéon-Sorbonne, Paris, France
e-mail: lauranrg@gmail.com

H.W. de Regt et al. (eds.), *EPSA Philosophy of Science: Amsterdam 2009*,
The European Philosophy of Science Association Proceedings 1,
DOI 10.1007/978-94-007-2404-4_23,

morphological and macroevolutionary patterns than is usual in the Synthetic framework. Accordingly, an associated claim is that microevolutionary *processes* cannot explain these morphological phenomena, and two new kinds of processes have been proposed to deal with them. One suggests that non-observable processes such as the selection of higher order taxa may explain macroevolutionary patterns (Eldredge and Gould 1972). The other appeals to development: evolutionary developmental biology ('evo-devo') claims that phenomena related to the aforementioned morphological patterns cannot be fully understood unless *developmental* processes are considered (e.g. Alberch 1980, Gilbert et al. 1996, Hall 2003).

If developmental processes are taken into account, the meaning of patterns and processes and their relationship with description and explanation change in evo-devo with respect to the so-called 'received view' of evolution. Although conceptions of patterns and processes in the Modern Synthesis and evo-devo have been contrasted previously (e.g. Arthur 2000), little attention has been paid in the philosophy of biology to the internal debates on this issue *within* evo-devo. This paper aims to clarify how pattern and process are understood in this new synthesis of development and evolution.

In the first section, three different approaches to evolution and development are distinguished, according to the different descriptive and explanatory roles that pattern and process play in each one. In the second section we sketch some consequences for the philosophical analysis of two central topics in evolutionary biology: homology and variation.

23.2 Patterns and Processes in Development and Evolution

The dialectics between pattern and process as we analyze it has generated three approaches to investigating the relationship between ontogeny and phylogeny: (a) the transformational approach; (b) the morphogenetic approach, and (c) the process approach.

23.2.1 The Transformational Approach

What we call the transformational approach to developmental evolution (Table 23.1, A) dates back to the evolutionary embryology of the 19th century, illustrated in the work of Ernst Haeckel. In this *static* version of the transformational approach (Table 23.1, Ai), development was conceived as a sequence of discrete patterns corresponding to certain developmental stages, such as the shape and topology of an embryo (e.g. nauplius, pharyngula, gastrula) or its parts (e.g. the limb bud). The goal of the theory of recapitulation was to uncover the parallelisms between series of ontogenetic and phylogenetic patterns, in the belief that ontogenetic stages constitute a record of evolutionary patterns. Within this framework, the main epistemological goal of evolutionary embryology is the comparative description of developmental patterns in order to reconstruct evolutionary patterns: changes in

Table 23.1 Summary of the three approaches to pattern and process in developmental biology and evo-devo

	Patterns/processes approaches	Description	Explanation
A	**Transformational (pattern to pattern) approach**		
i	*Static discrete*	Development and evolution are described as a sequence of discrete patterns	Phylogeny (i.e. inheritance) is the cause of the conservation of ontogenetic patterns
ii	*Static continuous*	Pattern transformation is formalized as a continuous transformation in geometrical space (ii) and in time (iii)	The theory of transformations (D'Arcy Thompson) points to laws of growth governing shape development
iii	*Dynamic*		Changes in the rate or timing of developmental events (heterochrony) cause changes in phylogenetic patterns
B	**Morphogenetic (process to pattern) approach**		
i	*Mechanistic*	Patterns are the described phenomena	Developmental processes cause evolutionary patterns (Alberch). Homologues are explained by conservative mechanisms that constraint generative processes (Wagner, Newman and Müller)
ii	*Formal*		Homologous patterns are formally explained as morphological attractors (Thom, Striedter)
C	**Process approach**	Processes as characters: stable pathways of change (process homology) and diachronic change of stable processes	The evolutionary stability of developmental processes is explained by canalisation and homeorhesis (Waddington, Gilbert)
i	*Step approach*	Both processes (detached of the patterns they generate) and patterns are described as characters which can be homologized	Separation between ontogenetic and evolutionary causes (Scholtz)

developmental sequences are explained as caused by terminal addition (recapitulation), terminal deletion (paedomorphosis) and substitution (caenogenesis) of certain patterns, whereas heterochrony (differences in the timing of the appearance of patterns) and heterotopy (spatial displacement of patterns) constitute the exceptions to the biogenetic law.

Another transformational account of pattern-to-pattern transitions can be found in D'Arcy Thompson's classical work on growth and form (1942). Although his attempt is not directly related to evolutionary models, his original and highly influential approach offers a geometrical strategy (the so-called theory of transformations) for describing shape and how it changes, analyzing *continuous* spatial transformations among patterns (Table 23.1, Aii).

In the late 1970s, a new *dynamic* transformational approach emerged (Table 23.1, Aiii). This period constitutes the early years of evo-devo, when a considerable amount of effort was dedicated to exploring how heterochrony explains continuous changes in size and shape. The seminal work of this new approach was Gould's clock model (1977), a qualitative and static description of how heterochronic changes in ontogenetic patterns relate to phyletic trends. However, the way in which heterochrony is used in current evo-devo was established in a subsequent paper by Alberch and co-workers (1979), who developed a quantitative and dynamical method for describing how heterochronic changes in developmental processes (onset, cessation and rate of growth of a given structure, such as a salamander's tail) produce relative changes in size and shape that parallel evolutionary transformations.

The two versions, static and dynamic, of the transformational approach start with the identification of patterns in order to make phylogenetic inferences based on the developmental transitions that take place among them. Nevertheless, there are important differences in how each of them conceives description and explanation.

Whereas recapitulationists describe ontogeny as a *discontinuous sequence of patterns*, in which each developmental stage represents a discrete event in the development of an embryo, in heterochrony models ontogeny appears as a *continuous transformation of patterns* that cannot be sliced into discrete morphological stages. In this sense, the dynamic transformational approach may be seen as incorporating the time dimension within the continuous framework of D'Arcy Thompson's pattern transformations (which is still static, like Haeckel's). The change of perspective is made possible by the new role assigned to time in heterochrony models: while in the Haeckelian approach developmental and evolutionary times are just coordinate axes upon which successive patterns are ranged, in heterochrony models time belongs to the developmental system, acting as a parameter of the developing organ or part under study. In view of this dynamic character of heterochrony models, some authors feel compelled to say that, in them, 'the dynamic life cycle is taken to be the unit of study', and ontogenetic *trajectories*, not patterns, are compared (Kluge and Strauss 1985). Nonetheless, in heterochrony models, the organ or part under study needs to be already in place in order to model its temporal transformation. That is the reason why we locate this approach in the same category as the Haeckelian approach: although the static and the dynamic versions of the transformational approach conceive patterns differently (the first as static and discrete stages; the second as dynamic gradual trajectories), both consider pattern transformations as the phenomena to model. Regarding explanation, the dynamic approach inverts the Haeckelian perspective. While in the static transformational approach phylogeny (i.e. inheritance) is the cause of ontogenetic patterns (regarded as records of phylogenetic patterns), in the dynamic transformational approach ontogeny is not seen as a record of phylogeny, but rather as its cause (de Beer 1958). Heterochrony models explain the phylogenetic transformation of patterns as caused by ontogenetic transformations (i.e. changes in timing).

23.2.2 The Morphogenetic Approach

The aim of the morphogenetic approach to development and evolution is mainly to explain how patterns or structures come into being. Thus, here, patterns are the phenomena to be explained (*explanandum*), whereas developmental processes involved in their generation are their causes (*explanans*).

This approach emerged at the end of the 19th century among a new generation of experimental embryologists who strongly opposed the previous transformational view of evolutionary morphology (Table 23.1, Bi). According to this view, as indicated by one of its main practitioners, ‘an array of forms, following one after the other is really [. . .] no explanation’ (His 1874, 176; quoted from Gould 1977, 192). So-called ‘developmental mechanics’ (*Entwicklungsmechanik*) called for a new approach to development based on the study of the *mechanical* processes in charge of the generation of form, rather than on evolutionary patterns of structural change (Maienschein 1991).

During the 20th century, a formal theoretical parallel of the mechanical investigation of development appeared in efforts such as Turing’s on chemical morphogenesis (1952) and René Thom’s on structural stability (1977) (Table 23.1, Bii). Thom’s theoretical investigation of pattern stability used diverse modeling practices to capture properties of biological processes and patterns which are not dependent on their physical-chemical nature. Aiming to explain the emergence and destruction of morphologies, the so-called ‘dynamic structuralism’ conceived development as a dynamical ‘fight’ among ‘fields’ or ‘archetypes’ (temporally stable morphological attractors) that generates ‘geometrically stable configurations’ (Thom 1968, 166).

Finding themselves in the convergence of the mechanistic and formal morphogenetic approaches to development, some of the first evo-devo practitioners advocated a morphogenetic *explanation* of developmental evolution. Thus Alberch (1985) defends a dynamic view that takes into account the underlying developmental mechanisms, so that developmental sequences are not just series of discrete and conserved patterns, but rather processes marked by key developmental events, such as the bifurcation and segmentation occurring in the pattern formation of digits in frogs and salamanders (Alberch and Gale 1985). Developmental processes are considered to be governed by a set of ‘construction rules’ which underlie the properties of the developmental interactions (at the biochemical, cellular and tissue level) and are capable of generating a global pattern. Consequently, the evolutionary changes between two related morphologies 'must be searched for in terms of changes in the developmental rules of interaction or initial conditions, rather than in intermediate ontogenetic stages' (Alberch 1985, 51).

In short: whereas the transformational approach is restricted to comparing developmental stages and to testing whether they have been conserved or altered throughout evolution, the morphogenetic approach aims (experimentally and formally) to explain changes among patterns as a result of changes in generative processes.

23.2.3 The Process Approach

We refer to the last approach considered in this paper simply as the 'process approach' because, unlike the two previous ones, it considers processes to be ontological constituents that deserve to be described by themselves, not necessarily serving as explanations of patterns (Table 23.1, C).

The main advocate of this approach is Waddington, who, deeply influenced by Whitehead's philosophy of processes, demanded a new 'diachronic biology'. Waddington claimed that neither development nor evolution should be understood as a series of discrete patterns, because 'the organisms undergoing the *process* of evolution are themselves *processes*' (1968, our emphasis). In his view, organisms are developmental systems undergoing a process of becoming which is never achieved, but that constitutes their very essence. To be able to account for this essentially dynamic character of living organization, Waddington introduced several new terms such as 'creodes' (developmental pathways or trajectories), 'canalisation' (the ability of developmental systems to return to the creode in spite of perturbations), and 'homeorhesis' (the resulting stability of the developmental process) (see, e.g. Waddington 1957, and Gilbert 2000 for a review of Waddington's concepts). He does not deny the existence of temporary stable patterns, but the focus is on the stability of life as a pathway of change which is preserved despite changes of state.

Waddington's proposal has been recovered by current developmental biology and evo-devo, both by the epigenetic program and the one in developmental genetics (Carroll et al. 2001, Davidson 2001). The idea is that '[d]evelopment is ultimately a process, and its central "characters" are as much temporal as spatial' (Gilbert and Bolker 2001); neither 'dynamical patterns' (developmental characters, such as the primitive knot—the organizer for gastrulation in vertebrates, which are transient and whose component cells are constantly changing) nor 'patterns in time' (developmental processes such as cell division sequences or the establishment of body axes, as well as genetic pathways) can be fully understood from a pattern-based approach.

From this perspective, developmental processes (epigenetic processes and genetic pathways) should be considered as characters themselves, regardless of how they contribute to pattern formation. As a matter of fact, developmental processes share the classical properties of morphological characters, i.e. stability, modularity and homology (Gilbert and Bolker 2001): (a) they are *stable* and so can be modeled as coherent objects of research; (b) they are *modular*, since they can be dissociated from other processes; and (c) as stable and modular phenomena, they can be *homologized* and seen as fundamental components of the developmental toolkit of evolution.

Bearing in mind that a given process may give rise to several patterns and that a given pattern may be the result of different kinds of processes, some authors hold that each process or pattern can be studied as an independent character. What we have called the step approach (Table 23.1, Cii) means a conciliatory solution between pattern-based and process-based definitions of development and evolution. Scholtz defines a developmental step ‘as a describable and comparable (homologisable) pattern at any moment of development’ (2008, 147), understanding by pattern both spatial patterns and patterns in time. Under this view, developmental patterns and processes may be evolutionary characters, and processes must sometimes be described as detached from the patterns they generate.

23.3 Discussion: Homology and Variation

Our classification of the various conceptions of the role of patterns and processes in the description and explanation of development and evolution may shed some light on several key discussions in the philosophy of biology of our time. In the remainder of our paper we briefly outline several elements stemming from our classification, which are worth considering in relation to two classical issues of important philosophical scope: (a) the problem of homology, and (b) the question of the variation and variability of morphological characters.

23.3.1 Homology: The Evolutionary Conservation of Patterns and Processes

Homology refers to the conservation of morphological patterns, defined by their structural correspondence (topology and connectivity). The classical example is the tetrapod limb, whose basic osteological pattern has remained the same throughout evolution despite variations in function (swimming, running, flying), position along the anterior-posterior axis of the body, shape, and number of distal elements.

Neo-Darwinian evolutionary biology and evo-devo have different perspectives on the meaning of morphological correspondences that have led to two different concepts of homology: phylogenetic and developmental (Roth 1984, Amundson 2001, Brigandt 2007).

The phylogenetic or *taxic* concept of homology (e.g. de Pinna 1991) identifies homologies with synapomorphies, the term used in cladistics to refer to those features shared by different species because they derive from a common ancestor. This line of research does not analyze the causes underlying the conservation of homologous parts, because its goal is not to explain, but rather to reconstruct the phylogenetic tree. What the evolutionary classification of organisms needs is not an explanation of the origin and stability of patterns, but a proper characterization of patterns themselves (i.e. topological correspondence), in order to infer historical relations between them. Therefore, among the approaches reviewed in the previous section, the transformational perspective (in both its static and dynamical versions) is coherent with the aim of establishing phylogenetic homologies.

Nevertheless, morphogenetic perspectives of homology have traditionally tried to find definitions of homology that can explain the conservation of patterns by relating homologies to the process of development. The general idea underlying the morphogenetic approach to homologous parts is that they are preserved because they are products of common developmental processes (Roth 1984, Webster and Goodwin 1996). However, the developmental characterization of homology is not an easy task.

The main difficulty faced by the *developmental* or biological definition of homology comes from the fact that homologous characters do not always share a common ontogeny. In fact, developmental processes have been shown to be dissociable from the structures they generate (Roth 1991, Hall 1999, 21). At the genetic level, different pathways are recruited in evolution to regulate the generation of a given structure (Abouheif et al. 1997). At the epigenetic level, homologous structures (e.g. vertebrate eyes) can be generated from different cellular material, embryological sequences, and inductive mechanisms (Wagner 1989). Thus, homologous patterns can often be evolutionarily stable throughout changing developmental processes. This paradoxical fact means that we must be cautious about the morphogenetic approach that would, in principle, appear to offer the most promising path towards a developmental explanation of homology. In evo-devo, the challenge posed by the variability of developmental pathways generating homologues has led to two different reactions.

On the one hand, the process approach has interpreted the asymmetry between developmental processes and evolutionary patterns as an argument in favor of the autonomy of processes. From this perspective, developmental processes can vary and evolve independently, acquiring new developmental roles in the course of evolution (Abouheif et al. 1997, Gerhart and Kirschner 1997, Brigandt 2007).

In the step approach, the evolutionary independence of patterns and processes has two important philosophical consequences regarding teleology and typology (Scholtz 2004, 2005, 2008): (a) since there is no necessary causal relationship between ontogenetic stages, *teleology* is challenged: from an evolutionary point of view, developmental processes should not be considered as leading to a given pattern, but as characters in and of themselves; accordingly, adult morphology is not the result of development, it is simply one stage among many; (b) the evolutionary dissociability of patterns stands in contrast to *typological* concepts stressing the universal greater importance of early stages for setting up any kind of *Bauplan*, such as the phylotypic stage (Slack et al. 1993).

On the other hand, within the morphogenetic approach, in order to offer a developmental account of the conservation of homologous parts, some authors have introduced a distinction between the processes that explain the *origination* of parts and those that account for the *maintenance* of morphological patterns. Wagner (1989) argues that 'morphostatic' mechanisms (Wagner and Misof 1993) do not only allow developmentally individualized parts to be autonomous and to face epigenetic and environmental stimuli; they also constrain the phenotypic effects of genetic variation. In this sense, morphostatic mechanisms explain the evolutionary stability of homologous patterns and the variability of generative processes, and thus biological homology can be defined in terms of shared developmental constraints. Newman and Müller (2000) hypothesize a similar scenario in their explanation of the origin and maintenance of morphological organization: in a first phase, *generative processes* (of a mechanical and chemical nature) lead to the origin of certain patterns; in a second phase, *processes of integration* (such as genetic regulation) increase the autonomy of those structures from the generative processes. However, instead of defining homology in accordance with conservative mechanisms, the distinction between generative and conservative mechanisms has led these authors to recover the classical definition of homology, understood as 'a manifestation of structural organization that maintains identical building elements despite variation in their molecular, development, and genetic makeup' (Müller 2003, 58–59). Within the formal morphogenetic approach, Striedter defends a similar idea, defining 'epigenetic homologues' as 'corresponding valley bottoms (attractors) in the epigenetic landscapes' that 'have continuously reappeared in the ontogenies of individual organisms since their origin in a single population of ancestral organisms' (2000, 224).

It becomes clear how our distinction of the different approaches to pattern and process helps clarify the issue of homology: the transformational approach defines the patterns of structural identity and change necessary to identify the homologies that will be used in the reconstruction of the tree of life; the process approach favors a view in which processes can themselves be homologues; the step approach considers that both patterns and processes can be homologues; and finally, the morphogenetic approach can favor either a mechanical definition of homology based on conservative mechanisms constraining the variational effects of generative processes, or a dynamical structural definition based on the organizational or geometrical stability of homologues.

23.3.2 The Variability of Patterns and Processes

We have seen how the different approaches to pattern and process deal with the conservative dimension of evolution, mostly manifest in the phenomenon of homology. But how do they address the phenomenon of variation in development and evolution?

The general philosophical disapproval of typology and essentialism in biology has resulted in difficulties understanding the nature of variation at the morphological level. In contrast to the focus of the Modern Synthesis on genetic variation, the examination of variation at the morphological level is essential to those evo-devo approaches interested in the study of pattern. The transformational approach is concerned with the investigation of the discontinuous or continuous transformation of form in space and time. However, as we saw, one of its main weaknesses is that it is constrained to the study of variation of already existing patterns.

In contrast, the morphogenetic approach makes it possible to incorporate both the variation of existing forms and the emergence of new patterns. In this view, the understanding of morphogenetic *processes* explains *variability* (i.e. the variational properties of developmental systems) and, consequently, the bounded *patterns* of morphological variation. Thus, pattern formation is perceived as the same problem as that of morphological variation (Salazar-Ciudad 2008).

One of the difficulties of the process approach lies in how to conceive the possibilities of change of a stable process. This issue was particularly evident in a brief correspondence between Waddington and Thom (1968), in which they discussed how to study and model the dynamic stability of developmental processes. Perhaps the most salient aspect of this dialogue is that Waddington's diachronic view seems to require something that Thom's dynamic structuralism might not be able to provide: 'The distinction I want to make is between a regime (flux equilibrium) which remains unchanging throughout a period of time and a regime which is, at any time, stable, but which changes progressively as time passes' (Waddington 1968, 168). From this perspective, to account for the evolution of developmental pathways, we need to explain how processes that are stable (due to constraints governing the canalization of a trajectory) can at the same time evolve. Processes need to be investigated as subjects of change.

23.4 Conclusions

We have considered three different views of evolution and development in accordance with how they conceive patterns and processes, ranging from the more static structural perspectives to the most radical processual ones. This plurality of approaches reveals the richness of the debates within evo-devo. Unlike in the received view of evolution, in the developmental approaches to evolution patterns and processes cannot be unequivocally identified with description and explanation, particularly when the epistemic goals of evo-devo do not necessarily favor explanation over description. Our discussion of homology and variation shows that evolution and development affect each other in complex ways, indicating that both developmental patterns and processes can be considered as evolutionary traits subject to conservation and change.

Acknowledgements AE's research was funded by the MICINN (FFI2008-06348-C02-01/FISO & FFI2008-06348-C02-02/FISO) and both authors acknowledge funding by the Basque Government (IT 505-10).

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