A sound of flower: evolutionary teachings from complex systems

by

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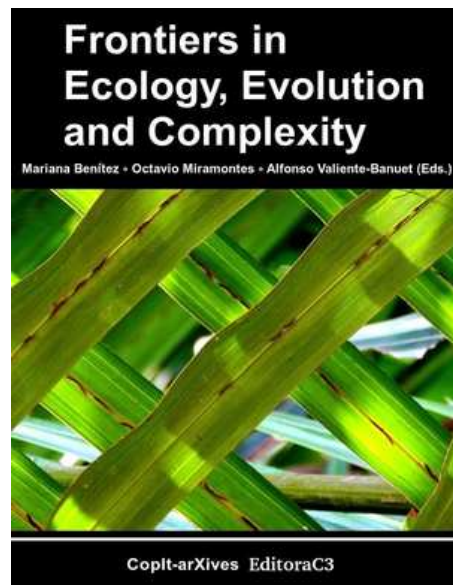
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Frontiers in Ecology, Evolution and Complexity

Contents

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Embedded in the mud, glistening green and gold and black,
was a butterfly, very beautiful and very dead.
R. Bradbury

El especialista «sabe» muy bien su mínimo rincón de universo;
pero ignora de raíz todo el resto.
J. Ortega y Gasset

1 Abstract

The new synthesis, mainstream theory of biological evolution, has serious problems when explaining certain biological phenomena. Reasons of this incapacity lie in Aristotelian functionalism, in implicit or explicit reductionism and in a disproportionate protagonist role of natural selection as the principal source of order in nature. The physical form of living creatures, according with functionalism, has a secondary, even negligible role in establishing natural prototypes. Form follows function. Thus existing structures are seeing as adaptations maintained and modified just by natural selection, they are exclusively the product of natural selection, the basic idea of the famous adaptationist program. Natural selection is a process of election which lead organisms to have a higher fitness; however, it depends on the existence of characters to choose from. Therefore, other process responsible for the creation of such traits must exist. Self-organization is presented as the previous force who determines the characteristics of the basic building units, relegating natural selection to a secondary role. A new evolutionary theory must be formulated that incorporates the teachings of Boolean genetic networks, self- organization, complex systems, chaos, with the recoverable traditional elements of the new synthesis.

2   Resumen

La síntesis nueva, teoría dominante sobre la evolución biológica, presenta serios problemas al tratar de explicar ciertos fenómenos biológicos. La raíz de esta incapacidad se debe principalmente a que se basa en un funcionalismo aristotélico, en un reduccionismo explícito o implícito y en darle un papel protagonista a la selección natural como fuerza ordenadora de la naturaleza. Si se analiza a los seres vivos desde una perspectiva funcionalista, la forma cobra un papel secundario, hasta despreciable, en el establecimiento de los prototipos naturales. La forma sigue a la función. Por ello las estructuras se perciben como adaptaciones mantenidas y modificadas sólo por la selección natural, son un producto exclusivo de ella, idea fundamental del famoso programa adaptacionista. La selección natural es un proceso de elección que encamina a los seres vivos a aumentar su eficacia; sin embargo, depende de que las características estén disponibles para elegirlas. Por lo tanto, debe de existir otro proceso responsable de crear las unidades de construcción naturales sobre las cuales, posteriormente, la selección natural actuará. Se presenta a la autoorganización como la fuerza previa que determina las características de las unidades de construcción, desplazando a la selección natural a un plano subordinado. Urge crear una teoría evolutiva nueva que incorpore las enseñanzas de las redes genéticas binarias, de la autoorganización, de los sistemas complejos, del caos, así como los elementos tradicionales recuperables de la nueva síntesis.

3   Introduction

According to Darwin's theory of natural selection, biological evolution must proceed in infinitesimal steps [1]. This is known as gradual evolution. Under these circumstances, the species concept has no reality. It is just an abstraction of the human mind. All recent species can be traced back by intermediate forms to the universal common ancestor of all life on Earth. With this perspective, the importance of the fossil record is overwhelming. The search of intermediate forms, the famous missing links, became an obsession because several groups of organisms did not have a connecting fossil with any known group. Man, birds and flowering plants, were the most remarkable. The apparently sudden origin of the flower, a conspicuous reproductive structure within the botanic world, was called by Darwin as an "abominable mystery" in a letter written to botanist Joseph Dalton Hooker in 1881. Nowadays, the fossil record is more complete, thus according with a gradualist point of view, the evolutionary history of the flower can be linked by a series of steps. However, it is not clear which is the common ancestor of flowering plants.

The new synthesis, the mainstream theory of biological evolution, born in the middle of the 20th century, was conformed with a great amount of facts from different biological disciplines: systematics, biogeography, development, paleontology, genetics, etc. [2]. The main ideas sustaining the new synthesis are natural selection, Mendelian inheritance, population genetics, and germoplasm theory. Other ideas, as the use and disuse of charac-

ters and the inheritance of acquired characters, life's tendency to complexity, orthogenesis, and macroevolution as a different process from microevolution, were denied. The theory can be resumed as: biological evolution is gradual, it occurs mainly by natural selection operating on variation among individuals within a population.

More than half a century has past since the new synthesis hatched, but still some fundamental questions have remained unanswered[1]. Despite the fact that some wrong ideas about life have been abandoned, such as Platonic essentialism, others, such as Aristotelian functionalism and reductionism continue contaminating the interpretations of the evolutionary process. The former postulates that form follows function. Characters of a living being are the result of a purpose, in that sense, functionalists are teleologists. As such, all parts of an organism respond to a task, and thus can be construed as being adaptations. The structure of any character depends on its purpose, its role. The latter, supposes that an entity is just the sum of its parts. It is possible to study a creature by dividing its body into pieces, examine each one separately, and finally, put them back together. The organism is the sum of its parts. The inception of the well criticized adaptationist program lies in these two philosophical positions [3]. Once a living being is finally constructed, natural selection explains how well it is adapted, but the new synthesis remains mute about the origin of evolutionary novelties [4]. Final causes (*telos*) may be studied with a functionalist vision, but not proximal causes (pera); moreover, final causes depend on proximal ones [5].

4   A case for *Shellock* Holmes

We live in a planet with an overflowing biodiversity. Sometimes the spectrum of different shapes of flowers, leaves, eyes, shells, seems infinite. Is nature really so prolific? Where are the limits to the biodiversity of forms, of nature's creativeness? Among the animal kingdom, only four groups have shells. They are the Phylum Brachiopoda, and three classes within the Phylum Mollusca: cephalopods, bivalves, and gastropods. The richness of shell forms is astonishing. Ranging from the baroque beauty of the delicate comb of Venus (*Murex pecten*), through a resemblance of a blade as in sword razor (*Ensis ensis*), to the mystic proportions of nautilus (*Nautilius pompilius*), creativity of nature looks endless. Hardly can we imagine new forms. At a first glance, the vast majority of possible shells forms have been created. Or have they? The new synthesis cannot respond this question. We need to know how shells are constructed, the secret rules behind them.

Raup [6] made a mathematical model in which the shape of a shell can be described with three parameters. The first quantity (W) affects the rate at which the diameter of the tube grows. The opening of the shell becomes wider with each rotation with higher values. The second (D), affects the distance of the center of the tube from the axis coiling.

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[1]The main reason of this situation involves the divorce and conflict between two plans of investigation: the study of development and the study of biological evolution, which occurred in 19th century.

With higher values the tube of the shell will form further from the coiling axis. Finally, the last variable (T), affects the distance of the center of the tube from the previous rotation along the axis of rotation. The shell will be taller with higher values. Any combination of these three parameters can be plotted in a cube, each dimension will represent one parameter. Inside this cube, each point is a combination of these parameters and represents a potential form of a shell. Any shell constructed by nature will be inside this cube. This space is called morphospace: the set of all possible morphs of shells (Figure 1). When we plot all known forms of these shields, only a small region of the cube is occupied. An enormous part of it remains empty. With this evidence, the new synthesis explains that natural selection is the responsible for the order found in the occupied zone. Shells are mainly, almost enterily, a product of this natural force. The explanation given from an adaptationist perspective is that there are no shells in the huge void of the cube because they are not adaptive, or some kinds of constraints avoid their existence. Even with Raup's model, these answers are extremely general. Much ado about nothing.
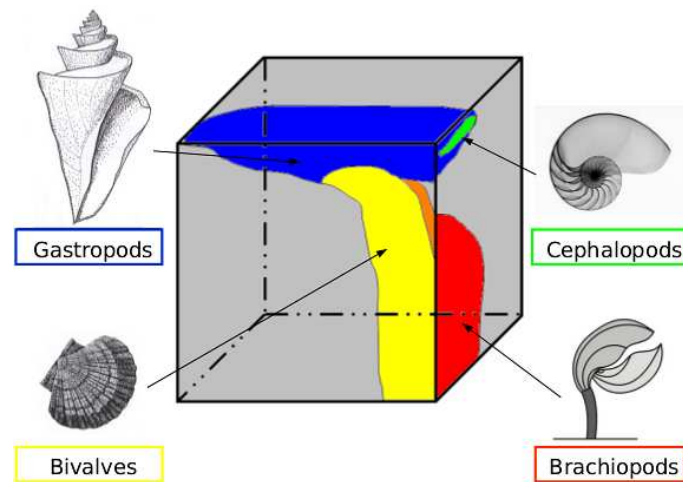

Figure 1: Shell morphospace. According to Raup's model, a shell can be constructed with three parameters, each point in the cube represents a particular combination of these measures, therefore a particular shell. Four groups of animals have shells, the zone they occupy is marked inside the cube with different colors.

5   Spices: self-organization, complex systems, and chaos

Some aggregations of organisms show extraordinary orderly behaviors. Shoals and flocks are typical examples. Starlings form a vast array of rich and complicated conformations as they fly over European skies. All birds fly seem to fly according to a general program, but there is no such plan. There is no leader who commands all birds to follow him. Order

emerges spontaneously. Local rules between each starling (going near other individuals, avoiding crash, etc.), generate the global pattern. This property present in some systems is self-organization.

Reductionist science has been very successful; however, its limits become evident when it deals with certain kinds of systems and phenomena. Certain groupings are not the sum of parts, thus, to study them we need to take into account the connections between their elements. For instance, studying an individual ant or a neuron will not reveal that a group of them, under specific conditions, and as a property of a particular number and the way they are connected, can generate an anthill or consciousness. These properties emerge from the interaction of the elements and cannot be anticipated with a reductionist point of view. A system whose dynamical properties cannot be understood without acknowledging its connections is a complex system.

Certain processes show a messy relation between their inputs and their outputs. Sometimes this apparent absence of cause or rules is called chance. Moreover, little variations on the inputs can produce radically different results. But if the initial conditions are exactly the same, the final outcomes will be identical. A deterministic dynamic system with high sensibility to initial conditions is chaotic.

6 A, B, C, D, E, F, Genes

A wealth of data on the molecular genetic mechanisms underlying different aspects of flower development have accumulated during the last two decades. The genes controlling cell-fate determination during floral organ specification have yielded the so-called ABC model of flower development that was derived from genetic analysis of floral organ homeotic mutants in two plant species used as study systems: *Antirrhinum majus* L. and *Arabidopsis thaliana* (L.) Heynh. [7]. These species have the stereotypical floral arrangement of almost all eudicotyledoneous flora[2], with sepals in the outermost whorl, then petals, stamens, and carpels in the flower center. The ABC model states that the identities of the floral organ types are established by combinations of genes grouped in three main classes, A, B, and C. A genes alone determine sepal identity; A plus B, petal identity; B plus C, stamen identity; and C alone, carpel identity (Figure 2). Additionally, A and C genes are mutually exclusive. The ABC model has been gradually expanded to include D class and E class genes, which are necessary to produce ovules and floral whorls, respectively [8].

However, the ABC model does not provide an explanation for how such combinatorial selection of gene activity is established during floral organ primordia specification, and how the spatio-temporal pattern of ABC and non- ABC gene expression is estab-

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[2]Among 257,000 species of flowering plants there are just two that have an inverted order of its reproductive whorls: sepals, petals, carpels and stamens. These plants are *Lacandonia schismatica* E. Martínez & Ramos, and *L. brasiliana* A. Melo & M. Alves.
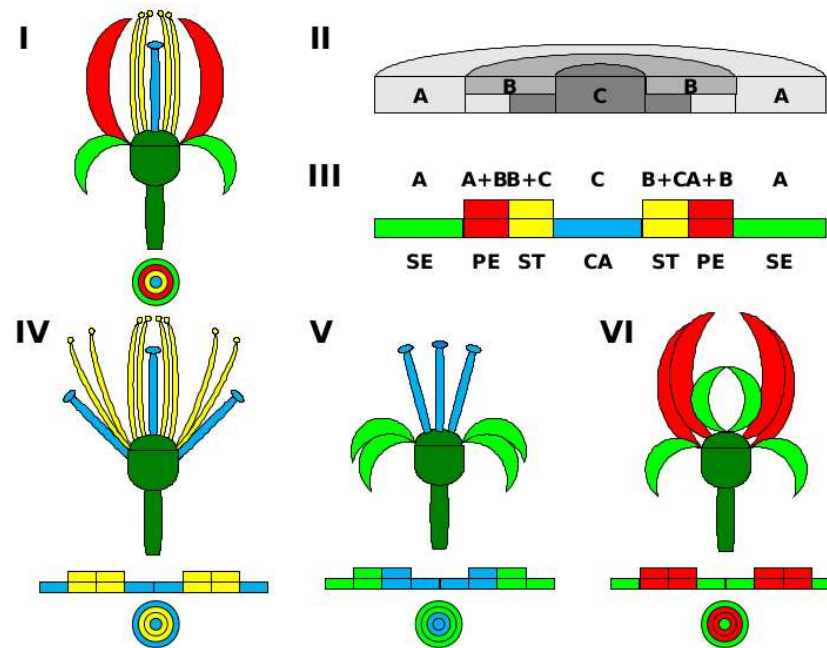
Figure 2: ABC model. I) Diagram of a wild flower with its four floral organs: sepals in light green, petals in red, stamens in yellow, and carpels in blue. Below: Transverse cut of the stem showing the concentric influence zones of ABC genes colored according to the floral organ produced. II) Influence zones of the ABC genes in the stem. III) Influence zones of ABC genes depicting which kind of floral organ they produce SE- sepal (light green), PE-petal (red), ST-stamen (yellow), CA-carpel (blue). IV) An *A* mutant produces stamens instead of petals, and carpels rather then sepals. V) A *B* mutant produces sepals instead of petals, and carpels instead of stamens. VI) A *C* mutant produces petals instead of stamens, and sepals rather than carpels.

lished. Furthermore, the conserved pattern of floral organ determination and the overall conservation of the ABC gene patterns of expression among eudicotyledoneous species suggest a robust mechanism underlying such combinatorial selection of gene activities. The ABC model by itself does not provide an explanation for such robustness either. The ABC model is purely narrative.

7   The oracle speaks

Inspired by the works of Jacob and Monod [9] about genetic regulation in prokaryotes, Kauffman [10] proposed that genetic systems can be modeled using Boolean or binary networks. Nodes represent genes. Links designate the interactions between them and symbolize how the products of a gene can activate or suppress the activity of other genes.

If a gene is active, it will be represented by a number one, otherwise it will be a zero. The state of a gene at any time will be determined by the combination of the states of all genes from which it receives information according to the equation:

$$G_N(t+1) = f_N(G_{N1}(t), G_{N2}(t), ..., G_{NK}(t)),\qquad(1)$$

where $G_N(t+1)$ is the state of gene N at time $t+1$, $(G_{N1}(t), G_{N2}(t), ..., G_{NK}(t))$ are the states of the K genes at time t that regulate the activity of gene N, and f_N is the logical rule associated with gene N. The total number of combinations is equal to 2^N, where N is the number of genes. Each of these combinations is called a configuration, and the set of all possible configurations of a network conforms the Ω space.

At $t+1$, each configuration has two possible destinies according to logical rules: it may transform into another configuration or rest unchanged. At long term, the system dynamics will attain one or more configurations. These stable configurations are attractors. An attractor composed by just one configuration is called a point attractor, otherwise it is a cyclic attractor, and the number of configurations that form a part of it are its period. The set of all configurations that end in the same attractor, either point or cyclic, are its basin of attraction. Basin attraction sizes can range from just one configuration to the entire Ω space (See example in Figure 3) [11]. Point attractors can be interpreted as cell types or characters. All other configurations are transient, fugacious, thereby, natural selection is unable to detect and choose them.

8 The symphony of flowers

According to the ABC model, certain genes are necessary to build a flower. If these genes are knocked out in the inflorescence, the plant will not produce this structure, rather, it will just develop an aggregate of leaves. Additionally, if the ABC genes are ectopically expressed in a leaf, no flower is generated; therefore, there must be more genes involved in flower formation. Based on experimental data Álvarez-Buylla and collaborators have delimited these genes, inferred their logical rules and modeled dynamics of the system. On a first approach [13] the network was not totally binary; 7 of 13 genes had three states. Finally, the network was translated to a full binary genetic network [14]. Of the total number of initial combinations ($2^13 = 8192$), the network attained 10 attractors, which coincide with the gene-expression profiles documented experimentally in cells of *A. thaliana* inflorescence meristems and floral organ primordia (Figure 4), and it also reproduces the gene-expression patterns documented in mutants[3].

When all outputs of the logical rules are systematically mutated, the vast majority of these point mutations (83.76%) conserved exactly the same 10 attractors originally obtained (we call this kind of change a neutral mutation). The other fraction obtained differ-

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[3]The last update of the floral network has subtle variations, but they do not alter the number of attractors or the overall behavior [15]
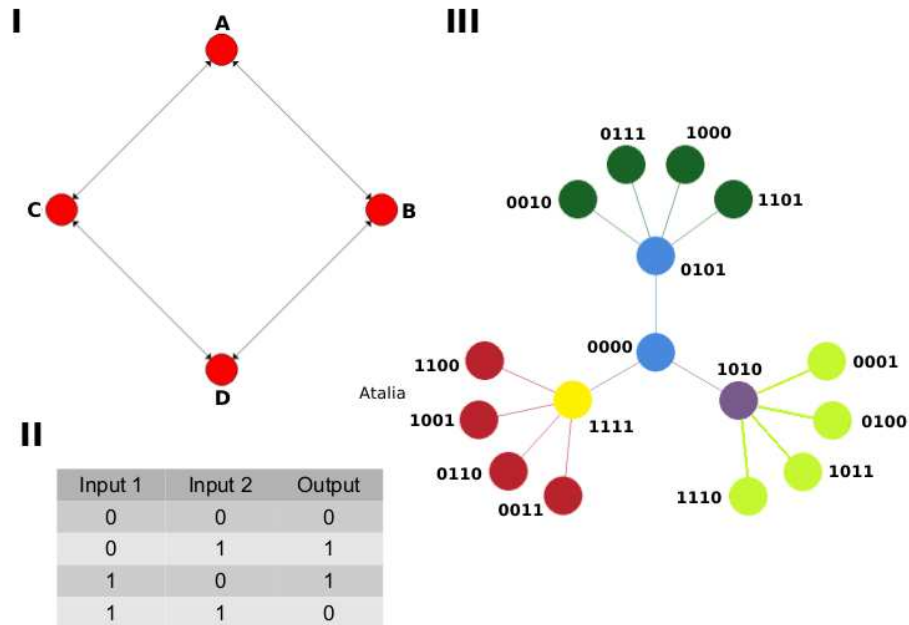
Figure 3: I) Network topology. II) Logical rule for all nodes. Every node has two inputs (ie. *A* receives information from *B* and *D*). The state of node *A* depends of the states of nodes *B* and *D*, and the logical rule of *A*. For example, if $B = 0$ (input 1) and $D = 1$ (input 2) then $A = 1$. III) System dynamics. The omega space is conformed by 16 configurations. Finally, all of them reach the same attractor at the center (0000), which is a point attractor. Colors are meaningless. Simulations and graphics were made using Atalia software [12].

ent combinations of attractors: 8.76% produced the same 10, plus new different attractors (an opportunistic mutation); 3.87% generated not all the original attractors, that is less than the original 10 (a reactionary mutation); and 3.60% created less than the 10 original attractors, but new attractors were obtained (an intrepid mutation) [16].

This behavior supports the idea that biological networks must be very robust in order to contend with most mutations, but at the same time they require to be a little flexible so that they can have the possibility to change. An absolutely robust network cannot evolve, it is frozen. In the other extreme, the dynamics of a completely flexible network is as a *tabula rasa* where with each alteration, the system cannot retain beneficial mutations or characters. Ii is like living in a perpetual revolution. This intermediate behavior lands in the zone called the edge of chaos [17] and exhibits criticality. Derrida's curve is another way to test this out [18].
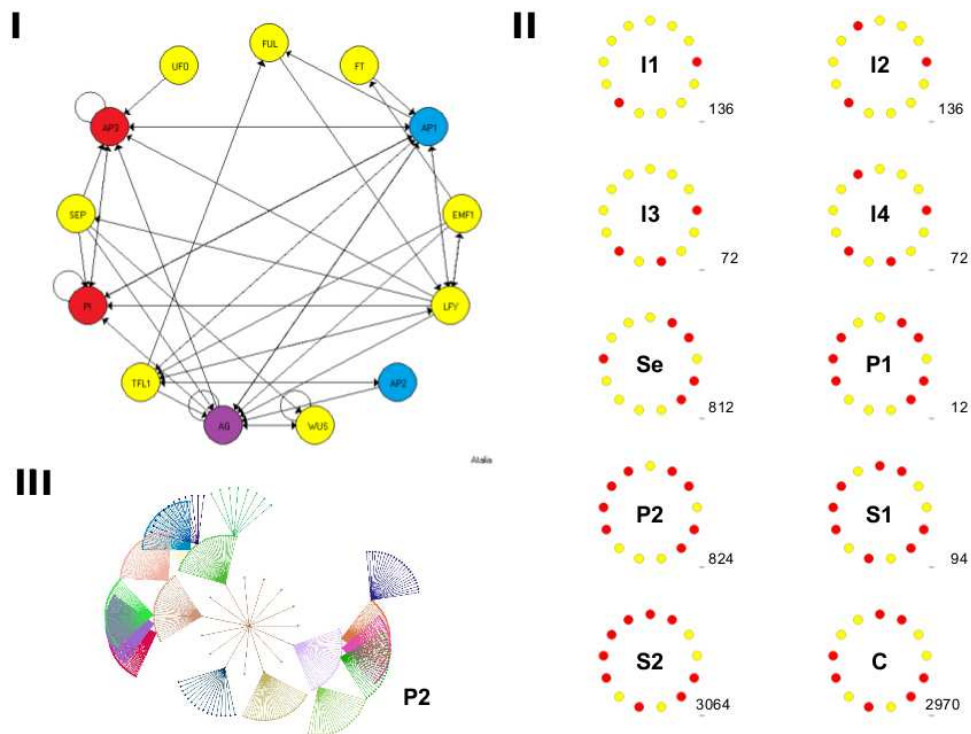
Figure 4: I) *A. thaliana* floral network. *A* genes are colored in blue, *B* genes in violet, *C* genes in red. II) From 8,192 total configurations just 10 are attractors. The figure shows each attractor configuration, nodes in red are active, nodes in yellow are inactive. Letters inside the circle of nodes are the floral organ which corresponds to that attractor: I- inflorescence, S-sepal, P-petal, St-stamen, C-Carpel. The number at the lower right corner is the size of the corresponding basin of attraction. Note the huge basins of attraction for the reproductive structures. III) The basin of attraction of Petal-2 attractor comprised 824 configurations. Each dot represents a configuration. The central node is the attractor. Simulations and graphics were made using *Atalia* software [12].

9   Coda

The Ω space is analogous to morphospace. Comprises all possible genetic configurations: the "geneconspace". Genetic networks model answers for phenomena that the new synthesis cannot account for. It explains why immense parts of the morphospace is empty, where most configurations are unstable, it identifies clearly which are the forbidden zones of this space. It gives priority to form over function, organization over selection.

Binary genetic networks help us understand some fundamental evolutionary properties. First, there is a preceding force of order to natural selection which dictates what

is stable, what can exist. Natural selection is subjugated by it. Self-organization creates, natural selection shades. This is consistent with developmental studies in which natural selection is removed, but order prevails [19]. Nevertheless, natural selection retain its combinatorial power. Second, several biological systems cannot be understood under the assumption that they are just the sum of their parts. Third, in spite of the robustness of genetic networks and their deterministic behavior, they change chaotically, thus minor alterations to genomes can produce large and unexpected modifications of the organisms and their environments [11]. This is a warning to the indiscriminate and irresponsible use of genetic engineering and transgenic plants and animals.

Key elements and properties of self-organization, complex systems, and chaos, must be taken into account to construct a new evolutionary theory, in which adaptive landscapes, fitness, morphospaces, geneconfspaces, attractors, and system dynamics, are combined together into a new paradigm of biological evolution [20].

Furthermore, this interpretation has connotations of ontological ilk about causality in nature. Life´s contingency may be no more than chaos with camouflage (but see [21]).

10   Bibliography

[1]   C. Darwin, *The origin of species by means of natural selection: or, the preservation of favored races in the struggle for life*.   Culture et Civilisation, Bruxelles, 1969.

[2]   J. Huxley, *Evolution. The Modern Synthesis.*   London: George Alien & Unwin Ltd., 1963.

[3]   S. J. Gould and R. C. Lewontin, "The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme," *Proceedings of the Royal Society of London. Series B. Biological Sciences*, vol. 205, no. 1161, pp. 581–598, 1979.

[4]   S. Løvtrup, *Darwinism: the refutation of a myth*.   Croom Helm London, 1987.

[5]   Á. Chaos, "La evolución biológica y el desarrollo," in *Biología orgánica*.   Facultad de Ciencias, UNAM, Mexico, in press.

[6]   D. M. Raup, "Geometric analysis of shell coiling: general problems," *Journal of Paleontology*, pp. 1178–1190, 1966.

[7]   E. S. Coen and E. M. Meyerowitz, "The war of the whorls: genetic interactions controlling flower development," *Nature*, vol. 353, no. 6339, pp. 31–37, 1991.

[8]   M. C. Dornelas and O. Dornelas, "From leaf to flower: revisiting goethe's concepts on the¨ metamorphosis¨ of plants," *Brazilian Journal of Plant Physiology*, vol. 17, no. 4, pp. 335–344, 2005.

[9] F. Jacob and J. Monod, "Genetic regulatory mechanisms in the synthesis of proteins," *Journal of Molecular Biology*, vol. 3, no. 3, pp. 318–356, 1961.

[10] S. A. Kauffman, "Metabolic stability and epigenesis in randomly constructed genetic nets," *Journal of Theoretical Biology*, vol. 22, no. 3, pp. 437–467, 1969.

[11] ——, *The origins of order: Self-organization and selection in evolution*. Oxford university press, 1993.

[12] Á. Chaos, "Atalia. version 2. software for binary network analysis." 2011. [Online]: http://web.ecologia.unam.mx/achaos/Atalia/atalia.htm

[13] C. Espinosa-Soto, P. Padilla-Longoria, and E. R. Alvarez-Buylla, "A gene regulatory network model for cell-fate determination during arabidopsis thaliana flower development that is robust and recovers experimental gene expression profiles," *The Plant Cell Online*, vol. 16, no. 11, pp. 2923–2939, 2004.

[14] A. Chaos, M. Aldana, C. Espinosa-Soto, B. G. P. de León, A. G. Arroyo, and E. R. Alvarez-Buylla, "From genes to flower patterns and evolution: dynamic models of gene regulatory networks," *Journal of Plant Growth Regulation*, vol. 25, no. 4, pp. 278–289, 2006.

[15] E. R. Alvarez-Buylla, M. Benítez, A. Corvera-Poiré, Á. C. Cador, S. de Folter, A. G. de Buen, A. Garay-Arroyo, B. García-Ponce, F. Jaimes-Miranda, R. V. Pérez-Ruiz *et al.*, "Flower development," in *The Arabidopsis Book*. American Society of Plant Biologists, 2010, vol. 8.

[16] Á. Chaos, "Importancia biológica y evolutiva de la estructura y de la dinámica de redas genéticas pequeñas: modelos de simulación inpsirados en redes reales," Ph.D. dissertation, UNAM. Mexico, 2010.

[17] S. A. Kauffman, "Antichaos and adaptation," *Scientific American*, vol. 265, no. 2, pp. 78–84, 1991.

[18] E. Balleza, E. R. Alvarez-Buylla, A. Chaos, S. Kauffman, I. Shmulevich, and M. Aldana, "Critical dynamics in genetic regulatory networks: examples from four kingdoms," *PLoS One*, vol. 3, no. 6, p. e2456, 2008.

[19] P. Alberch, "The logic of monsters: evidence for internal constraint in development and evolution," *Geobios*, vol. 22, pp. 21–57, 1989.

[20] Á. Chaos, *Cazadores de monstruos. Monstruos esperanzados y sistemas complejos. Evolución y autoorganización*. UACM, Mexico, 2012.

[21] E. R. Álvarez-Buylla, Á. Chaos, M. Aldana, M. Benítez, Y. Cortes-Poza, C. Espinosa-Soto, D. A. Hartasánchez, R. B. Lotto, D. Malkin, G. J. E. Santos *et al.*, "Floral morphogenesis: stochastic explorations of a gene network epigenetic landscape," *Plos One*, vol. 3, no. 11, p. e3626, 2008.