The multiple directions of evolutionary change

Diego Rasskin-Gutman* and Borja Esteve-Altava

Summary

The theory of Punctuated Equilibria challenges the neo-Darwinian tenet that evolution is a uniform process. Recently, an article by Hunt[1] has found that directional change during the evolution of a lineage is relatively small (occurring only in 5% of 250 analyzed traits). Of those traits that were shown to follow a trend, size was more likely to show gradual changes, whereas shape changes were more random. Here, we provide a short view of the nature of evolutionary trends, showing that directional change within lineages and among clades provides valuable evolutionary information about the processes involved in their generation. ***BioEssays*** **30:521–525, 2008. © 2008 Wiley Periodicals, Inc.**

Trends in evolution

When Edward D. Cope, the famous American Paelontologist studied the evolution of Cenozoic equids in the 19th century, he discovered that there was a steady increase in body size through time.[2] This general trend towards body size increase, nowadays known as Cope's Rule, has been studied and tested in numerous lineages with different statistical results.[1,3] Despite its lack of universality, it remains, until now, as one of the most pervasive general evolutionary arrow. Cope's discovery was a reflection of a search for laws, or principles, which were viewed in those times as a valid pursuit in Science (to be fair, it still is); in biology, however, the discovery of law-like phenomena has proved to be a little more difficult than in physics or chemistry. Trends are characterized by a recognizable sequence of parts or events that change in a given direction; in other words, a trend is a pattern. Trends can be found at all levels of the biological organization, from molecules to anatomy. In addition to Cope's rule, other trends from which empirical laws have been derived are, for example: (1) power law rules of allometry, with the alleged existence of an almost universal 3/4 proportional exponent that relates mass and metabolic rates ($B = aMb$, where B is any physiological variable, M is the mass of the organism, a is a coefficient that is taxon specific, and b is the famous 3/4 allometric exponent), (2) ecomorphological rules of body mass to latitude relation, such as Bergman's rule, and (3) symmetry and serial repetition rules in the body plan of bilateral animals.[4–6] In addition, general trends towards increasing complexity have been reported repeatedly.[7]

Because of their level of generality, touching both tempo and mode of the dynamics of change through time, evolutionary trends remain as one of the most fascinating and problematic issues in evolutionary biology.[8] Major efforts in the study of evolutionary trends have been focused in rates of evolution. In contrast, the direction of change has been often misunderstood or poorly systematized.[9] In the past 25 years, interest in the directionality of evolutionary change has increased, and different aspects of it have been extensively discussed.[1,3,10–12] Moreover, with the advent of comparative genomics, new trends in genomes complexity are being discovered.[13,14]

Whereas research has been focused in providing these phenomenological evolutionary laws with a populational genetic underpinning,[15] stressing the role of "externalist" adaptational forces, more "internalist" causes based on heterocronies and/or heterotopies can also be invoked as causal mechanisms.[16–18]

Punctuated equilibria challenges trends

Directionality in evolution is deeply embedded in Darwin's Theory of Evolution by means of Natural Selection, since gradual, uniform, changes imply a progressive trend leading to an increase in fitness in a lineage. In Darwin's own words: "And as natural selection works solely by and for the good of each being, all corporeal and mental endowments will tend to progress towards perfection."[20] The neo-Darwinian synthesis endowed this uniformitarian view with a mechanism based on allele frequency change in the genetic pool of a population. However the idea of "progress" was correctly abandoned; rather, it was then understood that any idea of being "better" or "worse" is related to an ever-changing fitness landscape, suggesting the metaphor of the Red Queen: always running to be able to stay in the same place.[21] Under the neo-Darwinian framework, large-scale trends are viewed as an extrapolation of micro-evolutionary processes occurring at population levels, where phyletic gradual transformation of

Theoretical Biology Research Group, Institute Cavanilles for Biodiversity and Evolutionary Biology, University of Valencia, Spain.
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*Correspondence to: Diego Rasskin-Gutman, Theoretical Biology Research Group, Institute Cavanilles for Biodiversity and Evolutionary Biology, University of Valencia, Apartado Postal 22085, 46071 Valencia, Spain. E-mail: diego.rasskin@uv.es
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species generates an evolutionary trend when selective pressure remains constant.[22]

Two major concepts clash head on with any necessity for directional trends throughout evolution. The first one takes on the neo-Darwinian synthesis, adding the Neutral Theory of evolution by M. Kimura,[23] introducing genetic drift as one of the major mechanisms explaining evolutionary change. A constant and random process, such as the accumulation of point mutations without selection, is not compatible with the traditional concept of directional evolution. The second concept is more fundamental in nature and comes mainly from paleobiologists, who challenged the idea of such an uniformitarian process in the 1970s: their data fitted better with a saltationist model, where species show long periods of stasis followed by short pulses of big changes. When the Punctuated Equilibria hypothesis was proposed by Gould and Eldredge to explain the saltationist pattern of the fossil record, the gradual direction of phyletic change became almost meaningless. Under this paradigm, lineages do not change substantially during its lifetime, remaining in stasis or morphological equilibrium, until speciation occurs. The consequence is clear, no phyletic trend (anagenesis) can occur at all, and the inevitable direction of gradual evolution disappears. Evolutionary trends are viewed at a macroevolutionary scale, within the processes of cladogenesis, as a direction in traits inheritance during successive speciation events[24]. According to Gould[25] ''anagenesis in this sense is illusory, and almost always the product of accumulated cladogenesis filtered through a higher level process of species sorting''.

The directional modes of evolution

Nowadays the debate about tempo and mode in evolution is widely open. Recent work by palaeontologist Gene Hunt suggests that gradual directional trends are rare in the fossil record; only 5% of fossil sequences analysed from more than 250 morphological traits show a significant directional mode of evolution.[1,12] In this work, Hunt points out the existence of two major handicaps in the literature that makes the correct identification of the trait's evolutionary mode difficult. First, fitting a given evolutionary sequence to a gradual or a stasis mode of evolution is almost a subjective enterprise, the same traits can be interpreted to fit one or the other depending on the author. Second, few data have been analysed globally in a quantitative way. To solve both problems, Hunt proposes rigorous statistical models for the three modes of evolution: unbiased Random Walk (uRW), biased Random Walk (bRW) and Stasis Model (SM). Following a rich tradition in the quantification of morphological change,[26] each model can be quantified studying two major parameters: the mean and the variance of a feature within a lineage.

Gradual change in Hunt's models is encapsulated as either uRW or bRW, accounting for non-directional and directional change respectively. For directional change to occur, divergences accumulate steadily, but without assuming a constant rate of accumulation, generating evolutionary trends within lineages. In non-directional change, divergences do not accumulate because changes occur at random around the mean. While the mean remains equal to zero in uRW and the changes occur inside the variance, in directional change the mean tends to increase or decrease along the evolutionary sequence. The model for stasis assumes no net changes in the evolutionary sequence of lineages; it opposes to both gradual and directional changes.

Hunt assumes two traditional dichotomies: gradual change versus stasis, and directional change versus random walk. By combining both dichotomies we can obtain four directional modes of evolution: gradual random mode, gradual directional mode, random walk in stasis mode, and stasis directional mode (see Fig. 1). The first three modes have a statistical model of evolution in Hunt's schema, while the last

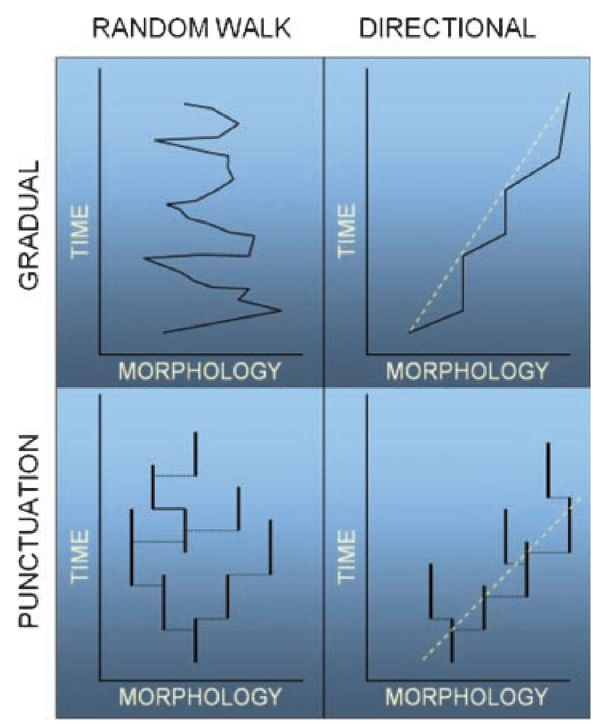

Figure 1. Schematic representation of the four possible modes of evolution combining the two classical dichotomies, random walk versus directional change, and gradual change versus punctuated equilibria change. **Upper Left:** Gradual random walk, anagenesis explores morphology without net change in the mean. **Upper Right:** Gradual directional change, anagenesis tends on average to vary the mean constantly. **Lower Left:** Random walk in stasis, cladogenetic processes explore morphology without preference of any morphology values. **Lower Right:** Directional stasis, cladogenetic processes tend to explore morphology with a preference in the direction of morphology values.

one has not been addressed in Hunt's work because it occurs between lineages, while these models apply to within lineages dynamics exclusively. The fourth direction, between lineages, allows the formation of evolutionary trends under the punctuated equilibria hypothesis, which was introduced by Gould and Eldredge[24] not as a gradual "product of slow, directional transformation within lineages" (anagenesis), but as a "differential success of certain species within a clade" (cladogenesis).

The statistical results of Hunt's work also show that size traits are more likely to be subject to a mode of gradual directional trend than shape traits, an aspect that might carry an intriguing evolutionary significance. Thus, it is tempting to speculate about a possible link between uRW, bRW, and SM by assuming that shape changes undertake pulses of transformation when the system cannot "absorb" the directional changes of size anymore during embryonic development. In other words, form follows size. This phenomenon could explain the unpredictability of size change throughout evolution; the shape of a trait will accommodate to a different stable configuration following a threshold-induced change in size.

Causal forces generating evolutionary trends: externalism versus internalism

Hunt suggests that several micro-evolutionary processes could account for each of the evolutionary modes. Thus,

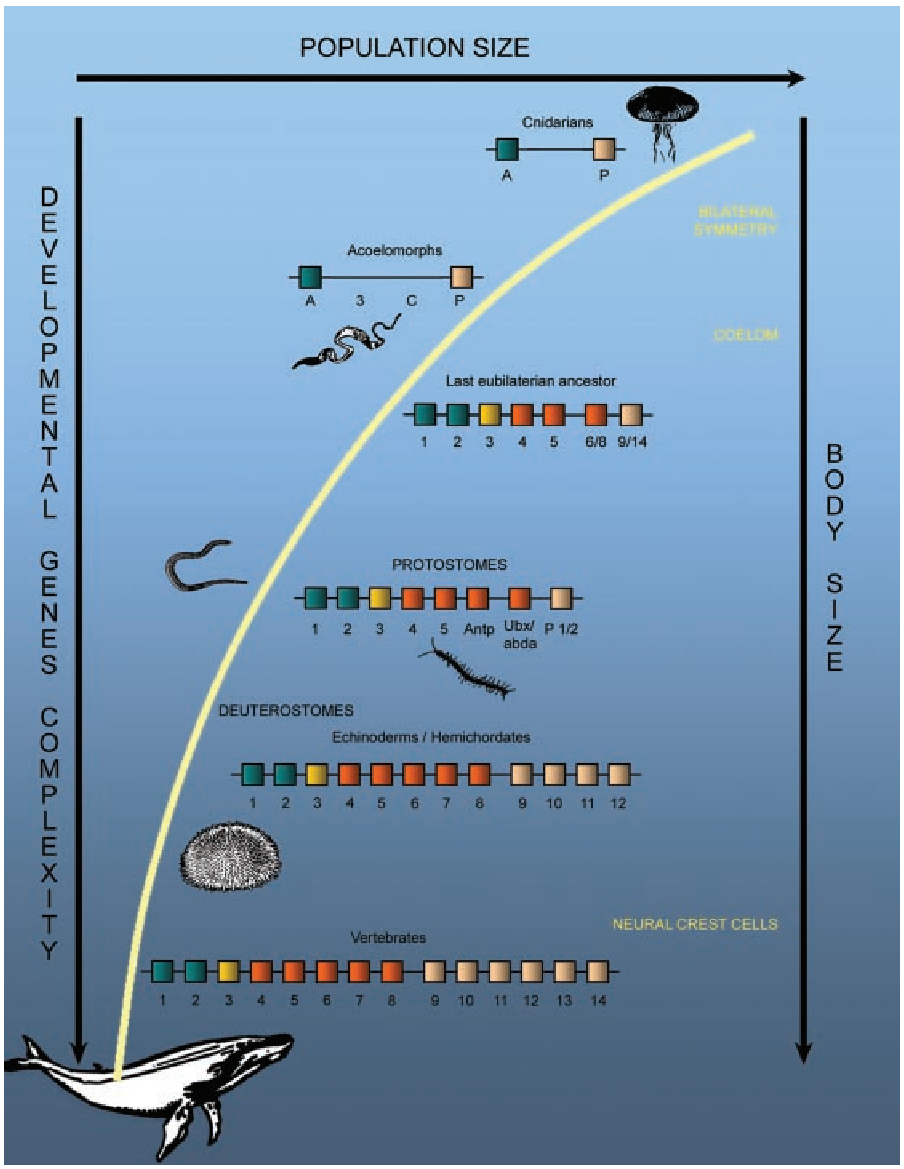

Figure 2. Relationship between the increasing in developmental complexity (illustrated by homeobox cluster genes complexity[42]) and body size, and decreasing in population size. Evolutionary trends in body and population size generate a trend in genomes complexity by means of genetic drift.[13,14] The genomic complexity in developmental genes allows the appearance of more-complex developmental programs, which can ultimately lead to the appearance of new morphologies. Thus, net increase in size is a causal force that generates not only new shapes but also new levels of genomic complexity. Shape and complexity follows size.

stabilizing selection can account for the stasis model and genetic drift for the unbiased random walk model. For evolutionary trends, it has been argued that the direction can be provided by the topography of the adaptive landscape framework.[1,27]. The adaptive landscape hypothesis predicts that a given morphology depends on the optimal value that it has in a fitness landscape. Optima points in a landscape can vary because of changes in external factors causing shifts in selective pressures. For example, adaptive peak movement in a directional change of temperature during the Cenozoic can generate a driven evolutionary trend such as increase in size through time in deep-sea ostracodes; incidentally, this model follows Bergmann's Rule, which can then be viewed as a causal mechanism accounting for Cope's rule.[28]

Internal causes related to developmental canalization and developmental constraints can account for directional changes during evolution even under a punctuated equilibria hypothesis. Internal processes are those in which the cause for evolutionary change is not related a priori to the environment. Many internal processes have been proposed, ranging from statistically to developmentally induced processes. Statistical constraints could be better understood as a diffusion event within a morphospace; the mean value of a given character will passively diffuse, moving away from the initial value, which acts as a lower bound.[29–31]. Developmental constraints are at the origin of directional change because any developmental step already present will tend to be integrated into developmental pathways,[32] and thus it will be hard to remove, generating a developmental entrenchment[33] or burden.[34] The stability of an acquired developmental stage shapes directional evolutionary changes, reducing the probability of change against that direction. Why a specific direction is taken by evolution remains still unknown, and may well be a matter of chance. But these internal processes explain why once a direction is chosen, a given directionality is maintained through time, generating an evolutionary trend.

Constraining evolution is not the only role of development. It is also the main internal causal process for evolutionary innovations and the occurrence of phylogenetic patterns.[35,36] Two developmental processes play a crucial role in evolution: heterochrony and heterotopy. Heterochrony, defined as a change in the speed of a developmental event can account for many evolutionary trends from ontogenetic-scale to phylogenetic-scale.[37,38] Heterotopy, a change in the location of developmental events without affecting the number of elements, has also great evolutionary impact.[19,39,40]

Body size links levels of biological organization

The importance of body size goes beyond changes in morphology; it also provides a link between genes, cells and development. A general increase in body size since the appearance of cellular life has been favored by natural selection because it has many ecological advantages, such as avoiding predation. At the same time, an increase in size in animals is correlated to population reduction,[41] identified by Lynch[13] as a crucial factor contributing to generate trends by passively increasing genome complexity by, for example, gene duplication. Thus, population size reduction in multicellular organisms, caused by body size increase, allows genetic drift mechanisms to gradually accumulate new genomic sequences without functionality. With time, some new genetic elements can acquire functions and start to be objects of natural selection; e.g. homeobox genes, and their successive duplication, have provided raw information material for complexity increase in animals.[42] But increase in body size also correlates with an increase in the net number of cell types, also called internal complexity by Bonner.[7] This cellular trend inevitably generates new occasions for development to find new morphogenetic processes (see Fig. 2). In other words, complexity follows size.

Conclusions

Evolutionary trends are the roads within which animal Baupläne have arisen, resulting from the intimate interaction of genetic drift, development and natural selection at the multiple levels of living organization. Hunt's work shows the statistical description of different modes of evolution in order to

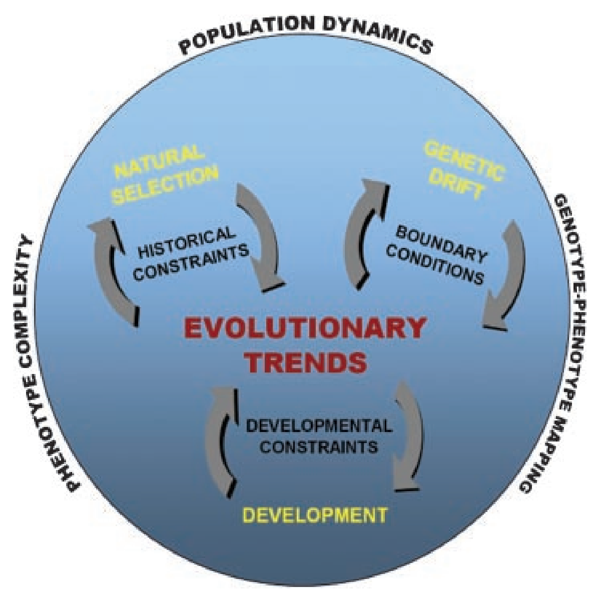

Figure 3. Conceptual relationship between evolutionary trends and the major processes of evolutionary change. Processes acting at populational level, such as natural selection and genetic drift, are causes of evolutionary trends following a top-down causality. Development at individual level generates trends as part of emergent bottom-up causality. At the same time, evolutionary trends generate other evolutionary trends due to historical constraints, developmental constraints and boundary effects.

compare evolving traits within lineages. The introduction of formalization in evolutionary modes studies allow the inference of the type of causal agent (internal or external, or both) for such an evolutionary trend. As such, formalization should also be carried out for every evolutionary trend, whatever its nature as anagenetic or cladogenetic. The canalization of developmental programs generates trends by biasing the possibilities of change. The evidences of the fossil record that suggests punctuated equilibria and evolutionary directionality across lineages can be explained by this developmental canalization as well as the relation between body size, population size, cell differentiation, genomic drift and natural selection. We can conclude that microevolution and macroevolution processes are related not as the direct extrapolation from the first to the second but as a causal cycle of interdependence of processes and patterns acting at genomic, developmental and ecological levels (see Fig. 3). Net increase in body size is a powerful causal force when entrenched in development throughout evolution, able to generate not only new shapes (morphological complexity) but also new levels of genomic and cellular complexity.

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