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Open Peer Commentaries

on Jorge Mpodozis's "Natural Drift: A Minimal Theory with Maximal Consequences"

Natural Drift: New Foundations for Understanding Evolution

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> Abstract • By focusing on the organism, and the systemic phenomenon of autopoiesis, natural drift as proposed by Maturana and Mpodozis provides an alternative foundation to natural selection for discussing adaptation and evolution. It takes into account basic structural considerations that have been sorely absent from mainstream thinking.

« 1 » Evolutionary thinking can be very different when coming from scientists with a background in neurobiology and constructivism, like Humberto Maturana and Jorge Mpodozis, compared to that from scientists with a conventional background in ecology and genetics. Firstly, Maturana and Mpodozis are probably more aware that the domain of an explanation must not be confused with the domain of the phenomenon to be explained, a distinction that becomes blurred in Theodosius Dobzhansky's widely accepted redefinition of evolution as the change in the genetic composition of populations (Dobzhansky 1937). Additionally, as organismal biologists, they are probably less inclined to overlook the level of the organism or consider it inconsequential, instead of focusing mainly on populations, genes, and the environment as a strictly external sieve for these genes. Rather, for these neuroscientists, the niche itself emerges from the actions of the organism, much like with our own cognitive world. It is the organisms that select their medium, and not the opposite.

« 2 » Maturana and Mpodozis propose a basic starting point that is lacking in mainstream evolutionary theory: an explanation of what is taking place at the level of the organism, namely, autopoiesis. This takes the phenomenon of adaptation into the logic of systems, and the changes that living systems may undergo without losing their autopoietic organization. The organism is the most basic level at which adaptation can be ascertained, and the logic is about all or nothing: either autopoietic organization is present, or the system is no longer autopoietic, losing properties such as autonomy and self-production, and ending in disintegration. Any change that does not end autopoiesis is, in a sense, neutral, or in other words, facultative. This has clear implications for how changes occur during evolution. As Jorge Mpodozis expresses in the target article, "aspects of the way of living, and of the corresponding ontogenic phenotype, that are constitutive (obligatory) for the derived species, are at the same time facultative for the ancestral species" (§33). In other words: at the outset, no change is ever obligatory (required for the conservation of autopoiesis). A natural question, therefore, is how do changes become obligatory? This topic deserves full development in an article of its own. However, I can anticipate that this is conceivable, because a new change in the medium or the organism can be operationally redundant with a pre-existing condition for autopoiesis; this allows the neutral loss (by drift) of such a pre-existing condition, upon which the new change becomes obligatory, as it alone is now fulfilling that role. This logic, where redundancy is implied in adaptive innovation, is akin to that discussed in the modern concept of exaptation, which describes how a biological structure can shift its function in a process that is different from natural selection (Gould & Vrba 1982; Gould 1997). The logic of redundancy is present within exaptation, where two different structures may perform the same function, while one of these structures can also perform a new, different function (Gould & Vrba 1982). Arguably, this makes exaptation highly systemic (context-dependent), and its importance and pervasiveness can be expanded in a framework based on systems theory and autopoiesis (rather than natural selection, where it remains largely ignored).

« 3 » By addressing the organism in the first place, Maturana and Mpodozis have made a necessary movement back to basic structural considerations, at the level of the organism. It is in this context that the simplicity of their proposal is so appealing. Mainstream evolutionary thinking has little use for basic concepts such as the ontogenic niche (namely, the developmental environment of an organism), but this is an essential part of the framework for discussing natural drift: change or conservation of an ontogenic phenotype in evolution cannot depend only on the total genotype, but must also depend on its history of encounters within the ontogenic niche. Development is not essential for discussing natural selection or population genetics. Indeed, following the arguments of Ernst Mayr (1961), development can even be downgraded to "proximal mechanisms" rather than being part of proper evolutionary mechanisms.

« 4 » By contrast, concepts such as the ontogenic phenotype and epigenic pathways are part of the essential framework of natural drift. As mentioned by Mpodozis (§37), some of these notions are so basic, they may seem like truisms, and yet, these structural considerations have important implications that are often ignored. In a recent article, we used them to discuss many phenomena of evolution in terms of natural drift, including several phenomena that have been overlooked by mainstream evolutionary theory, including genetic de-assimilation, neutral change in the ontogenic niche, and neutral epigenetic change in the total genotype. We also placed emphasis on how the epigenic field (of potential epigenic pathways) is not defined by the total genotype but, also, by the ontogenic niche (Vargas, Botelho & Mpodozis 2020).

« 5 » Let me conclude with some thoughts that appreciate the novelty of natural drift when compared to evo-devo (evolutionary developmental biology), considering the latter has attained mainstream success since the 1990s. In the late 1970s, evo-devo was revitalized by Stephen Jay Gould in his book *Ontogeny and Phylogeny* (Gould 1977). In this and many successive works, Gould presented evidence on how development influences the pathway taken by evolution. And while he questioned the pervasiveness of natural selection, Gould nevertheless maintained that natural selection should remain at the centre of evolutionary theory, despite his claim that other concepts should also be considered "pillars," without which evolution cannot be fully understood (Gould 2002).

« 6 » Many philosophers of biology have hailed the success of evo-devo as a significant departure from Neo-Darwinism, or even as a defeat of the latter. However, since the boom of molecular biology, many of the topics brought up by Gould seem to have faded into the background. For instance, most current research in evo-devo is focused on finding genetic changes behind evolutionary innovations. Indeed, it is more focused on the "devo" aspect of molecular genetics, than evolution or development at the organismal level (Diogo 2016, 2018). Many empirical scientists in evo-devo would also completely disagree that this field has replaced Darwinism: Instead, they would argue that evo-devo is set within an essentially Darwinian framework, that remains grounded on natural selection (Carrol 2005, 2006).

« 7 » This being said, one cannot deny that the emphasis on natural selection is no longer as hegemonical as in the 1950s and 1960s, and several researchers have declared we now live an "extended synthesis" (e.g., Pigliucci & Müller 2010). Some views within this extended synthesis are similar to those defended by Maturana and Mpodozis. For instance, more researchers now discuss epigenetic change (in the broad sense, including somatic and behavioural plasticity) as being important to the path taken by evolution. Then again, most of these researchers also consider that natural selection and population genetics continue to be the foundations for evolutionary thinking (e.g., Pigliucci 2008). This inevitably perpetuates the bias towards over-emphasizing genetic variation, and treating the environment as a sieve. Indeed, even Gould himself largely overlooked the role of epigenetic change. One may have the suspicion that the emphasis on natural selection in mainstream evolutionary theory derives mainly from the lack of any strong alternative as a foundational concept. This, however, would not apply to the framework of natural drift, whose starting point is autopoiesis and systems theory rather than natural selection, making it genuinely different from current trends within evo-devo or the extended synthesis.

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Alexander Vargas is an evolutionary biologist whose main contributions are about the origin and early evolution of birds, especially regarding their developmental evolution. He also revived interest in the neo-Lamarckian experimentalist Paul Kammerer (1880–1926), after pointing out specific resemblances between his experiments and modern experiments in transgenerational epigenetic inheritance. Since 2008, Vargas has run the laboratory of Ontogeny and Phylogeny at the Department of Biology, Faculty of Science, University of Chile. Since 2013, he has directed the Red Paleontológica U. Chile (Paleontological Network of U. Chile), whose members have described several fossil vertebrates new to science, including the transitional ankylosaur *Stegouros elengassen.*

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Darwinian and Autopoietic Views of the Organism

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> Abstract • Our goal is to illustrate that Darwinian and autopoietic views of the organism are not as squarely opposed to each other as is often assumed. Indeed, we will argue that there is much common ground between them and that they can usefully supplement each other.

« 1 » In his target article, Jorge Mpodozis defends an interesting alternative way of viewing the processes of development and evolutionary change that challenges the more traditional gene-centred perspective associated with Darwinian theorizing. However, we do not think that the mode of presentation, as a stark dichotomy between his view and the standard picture, is necessary or indeed helpful. Instead, we argue that both perspectives provide something useful for understanding evolution, and there is more common ground between them than he allows.

« 2 » In particular, we doubt that there are many contemporary defenders of the strong genetic determinism that he pits his view against. For example, the view that "envisages the process of development as the deployment of a set of instructions encoded in the DNA of some of the initial cellular components of a living being" (§17) seems like a straw man, one that any modern biologist is unlikely to endorse without acknowledgement of the range of other structures and processes that influence development. Even if biologists often idealize non-genetic processes away, that is not evidence, in itself, for a stronger metaphysical commitment to genetic determinism. Contemporary biologists such as Eva Jablonka and Marion Lamb (2020) recognize a variety of influences on ontogeny, phenotype, and inheritance, such as epigenetics and differential gene expression – even if they might disagree about how important they think these processes are. When Mpodozis states that "characters are not inherited, but recreated by the process of systemic reproduction" (§23), this does not appear at odds with mainstream thinking, since no one thinks that traits are somehow inherited whole, but rather that genetic inheritance provides a rough "blueprint" or, better, "scaffold" from which they are reconstructed in feedback-loops with the environment (Veit 2022a). It is thus hardly surprising that the specific outcome is highly sensitive to particular environmental conditions, gene expression, and other epigenetic factors. While the older metaphors are still persisting, the mainstream views of biologists have already shifted substantially in the last decades. Admittedly, Mpodozis's account is based on Maturana and Varela's theories in the 1980s when the mere mention of epigenetics was scorned and evolutionary developmental biology had not been developed yet into a thriving field. Nevertheless, things have changed and these changes are more congruent with his work than Mpodozis seems to think.

« 3 » Unfortunately, Mpodozis sets up his position as an absolute that stands in contrast with constructivist discourse:

> "Reproduction is a systemic process of conservation of a particular organism–medium relation, or way of living, and *not a genetic process* […] A lineage arises in the systemic reproductive conservation of a way of living and *not in the conservation of a particular genotype.*" (§1, italics added for emphasis)

« 4 » We would like to suggest a more fruitful middle ground that can take into account features of both views. For instance, while we agree with Mpodozis that "it is not possible to claim that any features that arise in the life history of an organism are [exclusively] genetically determined" (§1), neither is it the case that they are completely independent of genetic conditions. He admits that the genotype is something like a gatekeeper, constraining the space of possible structure and action, and it is here that we see the most common ground – the difference between the views starts to seem more like one of degree rather than kind. The degree to which these constraints, rather than developmental or epigenetic conditions,