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Stability-based sorting: The forgotten process behind (not only) biological evolution



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ABSTRACT

Natural selection is considered to be the main process that drives biological evolution. It requires selected entities to originate dependent upon one another by the means of reproduction or copying, and for the progeny to inherit the qualities of their ancestors. However, natural selection is a manifestation of a more general persistence principle, whose temporal consequences we propose to name "stability-based sorting" (SBS). Sorting based on static stability, i.e., SBS in its strict sense and usual conception, favours characters that increase the persistence of their holders and act on all material and immaterial entities. Sorted entities could originate independently from each other, are not required to propagate and need not exhibit heredity. Natural selection is a specific form of SBS-sorting based on dynamic stability. It requires some form of heredity and is based on competition for the largest difference between the speed of generating its own copies and their expiration. SBS in its strict sense and selection thus have markedly different evolutionary consequences that are stressed in this paper. In contrast to selection, which is opportunistic, SBS is able to accumulate even momentarily detrimental characters that are advantageous for the longterm persistence of sorted entities. However, it lacks the amplification effect based on the preferential propagation of holders of advantageous characters. Thus, it works slower than selection and normally is unable to create complex adaptations. From a long-term perspective, SBS is a decisive force in evolutionespecially macroevolution. SBS offers a new explanation for numerous evolutionary phenomena, including broad distribution and persistence of sexuality, altruistic behaviour, horizontal gene transfer, patterns of evolutionary stasis, planetary homeostasis, increasing ecosystem resistance to disturbances, and the universal decline of disparity in the evolution of metazoan lineages. SBS acts on all levels in all biotic and abiotic systems. It could be the only truly universal evolutionary process, and an explanatory framework based on SBS could provide new insight into the evolution of complex abiotic and biotic systems.

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1. Introduction

1.1. Theories on the origin of adaptations

The most important evolutionary discovery of Charles Darwin was probably the identification of natural selection (Darwin, 1859). This process offers the explanation of the origin and accumulation of adaptive, often functionally and structurally complex, characters in organisms. These characters enable organisms to effectively and often sophisticatedly react to the selective pressures of their environment, use its resources, and avoid its detrimental forces. Despite all of this, these adaptations that enable survival and successful reproduction of organisms in complex and changing environments originated through the "primitive" method of trial and

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http://dx.doi.org/10.1016/j.jtbi.2017.09.004 0022-5193/© 2017 Elsevier Ltd. All rights reserved. error, i.e., without the intervention of any sentient being or existence of a preliminary plan.

Explanations and solutions based on the principle of natural selection were applied in a plethora of other systems in the fields of natural science, technology and even humanities. Over the years, evolutionary biologists discovered that selection has several components and many forms, and that biological evolution is also driven and markedly affected by many other mechanisms, e.g. genetic drift, genetic draft, evolutionary drives, gene flow, and species selection (see e.g. Mayr, 2003). It was also demonstrated that numerous adaptive traits did not originate as biological adaptations but, exaptations, or even spandrels (see e.g. Gould, 2002). Moreover, the complex nature of genetic inheritance, various forms of non-genetic inheritance, and the evolution of multi-level metaadaptations (such as the ontogeny of metazoans) that affect the evolvability of lineages and canalize their ontogeny and anagenesis returned to the focus of evolutionary and developmental biologists in the last years (see e.g. Laland et al., 2015).

However, natural selection is probably a manifestation of a more general law that affects all material and immaterial entities in the universe, does not require replication and inheritance, and is usually called survival of the stable, according to the remark in the first chapter of Dawkins' book Selfish Gene (Dawkins, 1976, p. 13¹). At first, it sounds like a tautology: Changeable entities change, whereas stable or rapidly emerging entities accumulate and predominate in the system. Indeed, the claim that the most stable (or persistent) entity lasts the longest time is undoubtedly an axiom (Grand, 2001, p. 34–38; Pross, 2012; Shcherbakov, 2012; Pascal and Pross, 2014,2015) and this "law" thus seems utterly trivial, at least in a simple model. However, in the real world, coexisting entities interact in a complex manner and the consequent evolution of systems of interacting entities with variable and context-dependent persistence is all but simple (while still characteristic of the perpetual search for states of higher stability) (see e.g. Bardeen, 2009, or Pross, 2003,2004,2012; Wagner and Pross, 2011; Pascal and Pross, 2014,2015,2016, and references therein). As Shcherbakov (2013) concludes: "This principle - "survival of those who survive" - sounds as a tautology, but it is the great tautology: Everything genuinely new emerges through this principle."

Remarks analogical to Dawkins' survival of the stable were made also by several other researchers (e.g. Lotka, 1922a,b; Simon, 1962; Wimsatt, 1980; Van Valen, 1989; Michod, 2000; Grand, 2001; Maynard Smith and Szathmáry, 2010) whereas possible relations between natural selection and various forms of self-organization were analysed by Weber and Depew (1996). However, to our knowledge, Addy Pross and his colleagues elaborated the idea most profoundly (see e.g. Pross, 2003, 2004, 2012; Wagner and Pross, 2011; Pascal and Pross, 2014, 2015, 2016). The phenomenon itself is very general and probably applies to all fields that concern any form of biological or non-biological evolution. Researchers that touched it from various angles during their investigations called it e.g. natural selection in the non-living world (Van Valen, 1989), survival in the existential game (Rappaport, 1999; Slobodkin and Rapoport, 1974), contraction (Slotine and Lohmiller, 2001), Persistence Through Time of a lineage (Bouchard, 2008; Bouchard, 2011), thermodynamic stability (Pross, 2003,2004,2012; Wagner and Pross, 2011), the selection of long-lasting structures (Shcherbakov, 2012), sorting on the basis of stability or sorting for stability (Flegr, 2010, 2013), natural selection through survival alone (Doolittle, 2014), viability selection or selection on persistence (Bourrat, 2014), persistence principle (Pascal and Pross, 2014,2015,2016), ultrastability (Bardeen and Cerpa, 2015), eventually differential persistence or persistence selection (Doolittle, 2017). This loose conceptual embedding is probably related to the fact that only a few theoretical researchers (at least in the field of evolutionary biology) attribute great importance to this phenomenon. For example, Okasha (2006, p. 214), who comments on the topic more thoroughly, calls this phenomenon weak evolution by natural selection. According to him, this process cannot generate interesting adaptations and thus he considers it to be (in contrast with *paradigmatic evolution by* natural selection) uninteresting from the evolutionary viewpoint. Godfrey-Smith (2009, pp. 40 and 104), presents a similar opinion. He considers such an extension of the term "natural selection" (i.e., low-powered Darwinian process) essentially possible but artificial and basically useless. The opposite opinion has been much rarer. It was explicitly presented, e.g., by Bouchard (2011), Doolittle (2014,2017) or Bourrat (2014). Bourrat (2014) even demonstrated that this process can lead to some class of adaptations in numerical models of evolution. He stated that it could actually stand on the very beginning of biological evolution—original non-replicating entities differing only in their persistence could transform into genuine replicators by the means of this process.

In this paper, we argue that this evolutionary mechanism, which is currently underappreciated and mostly is not taken into account in efforts to explain the origin of characters of living organisms at all, acts upon all biotic and abiotic systems that undergo evolution. In fact, this process may be responsible for a wide range of adaptive traits. In the reaction to its weak conceptual embedding, we propose to call this survival of the stable (Dawkins, 1976, p. 13) or, more exactly, temporal manifestation of persistence principle (Pascal and Pross, 2014,2015,2016), i.e., the general tendency for more stable, persistent and unchangeable entities and characters in the system, unambiguously stability-based sorting (SBS) according to the conception proposed by Vrba and Gould (1986) and Gould (2002, p. 659). This term avoids any connotations that attribute the phenomenon only to material, immaterial, living or non-living entities, its confusion with natural selection, which we consider a specific manifestation of this universal principle (see Section 2.1), and its confusion with sorting based on any other kinds of criteria. We will clarify the relationship of SBS and selection more thoroughly in the next section. More particularly, we will show that selection is just one special manifestation of the general process of SBS (a relationship that was implied by numerous evolutionary-biological scholars of the role of persistence in nature mentioned above, e.g. Dawkins, 1976, Okasha, 2006, Godfrey-Smith, 2009, Bouchard, 2011, Doolittle, 2014, or Bourrat, 2014). However, despite being related in their essence, selection, as a special case of SBS, has markedly different evolutionary consequences. Therefore, because the aim of this article is predominantly to demonstrate and stress the different evolutionary consequences of the two processes (deeply understudied SBS in the strict sense and usual conception, and its special case, selection), we will consider SBS and selection as separate phenomena from now on.

2. Results and discussion

2.1. The relationship between selection and SBS

All forms of selection, including species selection, require selected entities to originate in reproduction or copying (and thus have an ancestor-descendant relationship) and exhibit at least some degree of inheritance of ancestor qualities (Gould, 2002; Okasha, 2006; Godfrey-Smith, 2009). SBS, on the other hand, does not require any of this. It takes place in all systems with history, i.e., evolution in the broad sense. SBS acts upon all material and immaterial entities regardless of their origin, even entities that originate independently of each other such as snowflakes, cosmic objects during the history of universe, memes, or mutually isolated civilizations. According to the fact that-by definition-unstable and changeable entities expire or change into something else whereas the stable and invariable entities persist, more and more increasingly stable variants of sorted entities accumulate in the system over time, whereas less stable variants gradually vanish. This is true even in the case that less stable entities originate more often in a studied system than their stable variants.

SBS and selection act both in open and growing systems, and in closed systems with a stagnating number of entities. For example, in the course of a snowstorm, the number of competing entities (snowflakes) is not limited and will constantly grow in the snow cover (an open system into which new snowflakes constantly arrive from the system's surroundings). In such a system, the number of less stable entities will constantly decline, but never reach zero

¹ "Darwin's 'survival of the fittest' is really a special case of a more general law of survival of the stable (...) The earliest form of natural selection was simply a selection of stable forms and a rejection of unstable ones. There is no mystery about this. It had to happen by definition."

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