

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

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## 13 Abstract

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

## 36 Keywords

37 Evolutionary theory; selection; static stability; dynamic stability; Frozen evolution

## 38 1 Introduction

### 39 1.1 Theories on the origin of adaptations

40 The most important evolutionary discovery of Charles Darwin was probably the identification  
41 of natural selection (Darwin, 1860). This process offers the explanation of the origin and accumulation  
42 of adaptive, often functionally and structurally complex, characters in organisms. These characters  
43 enable organisms to effectively and often sophisticatedly react to the selective pressures of their  
44 environment, use its resources, and avoid its detrimental forces. Despite all of this, these adaptations  
45 that enable survival and successful reproduction of organisms in complex and changing environments  
46 originated through the “primitive” method of trial and error, i.e., without the intervention of any  
47 sentient being or existence of a preliminary plan.

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

59 However, natural selection is probably a manifestation of a more general law that affects all  
60 material and immaterial entities in the universe, does not require replication and inheritance, and is  
61 usually called *survival of the stable*, according to the remark in the first chapter of Dawkins’ book

62 Selfish Gene (Dawkins, 1976, p. 13<sup>1</sup>). At first, it sounds like a tautology: Changeable entities change,  
63 whereas stable or rapidly emerging entities accumulate and predominate in the system. Indeed, the  
64 claim that the most stable (or persistent) entity lasts the longest time is undoubtedly an axiom (Grand,  
65 2001, p. 34-38; Pross, 2012; Shcherbakov, 2012; Pascal and Pross, 2014, 2015) and this “law” thus  
66 seems utterly trivial, at least in a simple model. However, in the real world, coexisting entities interact  
67 in a complex manner and the consequent evolution of systems of interacting entities with variable and  
68 context-dependent persistence is all but simple (while still characteristic of the perpetual search for  
69 states of higher stability) (see e.g. Bardeen, 2009, or Pross, 2003, 2004, 2012; Wagner and Pross,  
70 2011; Pascal and Pross, 2014, 2015, 2016, and references therein). As Shcherbakov (2013) concludes:  
71 “This principle – “survival of those who survive” – sounds as a tautology, but it is *the great tautology*:  
72 Everything genuinely new emerges through this principle.”

73         Remarks analogical to Dawkins’ *survival of the stable* were made also by several other  
74 researchers (e.g. Lotka, 1922a, b; Simon, 1962; Wimsatt, 1980; Van Valen, 1989; Michod, 2000;  
75 Grand, 2001; Maynard Smith and Szathmáry, 2010) whereas possible relations between natural  
76 selection and various forms of self-organization were analysed by Weber and Depew (1996).  
77 However, to our knowledge, Addy Pross and his colleagues elaborated the idea most profoundly (see  
78 e.g. Pross, 2003, 2004, 2012; Wagner and Pross, 2011; Pascal and Pross, 2014, 2015, 2016). The  
79 phenomenon itself is very general and probably applies to all fields that concern any form of  
80 biological or non-biological evolution. Researchers that touched it from various angles during their  
81 investigations called it e.g. *natural selection in the non-living world* (Van Valen, 1989), *survival in the*  
82 *existential game* (Rappaport, 1999; Slobodkin and Rapoport, 1974), *contraction* (Slotine and  
83 Lohmiller, 2001), *Persistence Through Time of a lineage* (Bouchard, 2008; Bouchard, 2011),  
84 *thermodynamic stability* (Pross, 2003, 2004, 2012; Wagner and Pross, 2011), *the selection of long-*  
85 *lasting structures* (Shcherbakov, 2012), *sorting on the basis of stability or sorting for stability* (Flegr,  
86 2010, 2013), *natural selection through survival alone* (Doolittle, 2014), *viability selection* or *selection*

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<sup>1</sup> „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.”

87 *on persistence* (Bourrat, 2014), *persistence principle* (Pascal and Pross, 2014, 2015, 2016), eventually  
88 *ultrastability* (Bardeen and Cerpa, 2015). This loose conceptual embedding is probably related to the  
89 fact that only a few theoretical researchers (at least in the field of evolutionary biology) attribute great  
90 importance to this phenomenon. For example, Okasha (2006, p. 214), who comments on the topic  
91 more thoroughly, calls this phenomenon *weak evolution by natural selection*. According to him, this  
92 process cannot generate interesting adaptations and thus he considers it to be (in contrast with  
93 *paradigmatic evolution by natural selection*) uninteresting from the evolutionary viewpoint. Godfrey-  
94 Smith (2009, pp. 40 and 104), presents a similar opinion. He considers such an extension of the term  
95 “natural selection” (i.e., *low-powered Darwinian process*) essentially possible but artificial and  
96 basically useless. The opposite opinion has been much rarer. It was explicitly presented, e.g., by  
97 Bouchard (2011), Doolittle (2014) or Bourrat (2014). Bourrat (2014) even demonstrated that this  
98 process can lead to some class of adaptations in numerical models of evolution. He stated that it could  
99 actually stand on the very beginning of biological evolution—original non-replicating entities  
100 differing only in their persistence could transform into genuine replicators by the means of this  
101 process.

102 In this paper, we argue that this evolutionary mechanism, which is currently underappreciated and  
103 mostly is not taken into account in efforts to explain the origin of characters of living organisms at all,  
104 acts upon all biotic and abiotic systems that undergo evolution. In fact, this process may be responsible  
105 for a wide range of adaptive traits. In the reaction to its weak conceptual embedding, we propose to  
106 call this *survival of the stable* (Dawkins, 1976, p. 13) or, more exactly, temporal manifestation of  
107 *persistence principle* (Pascal and Pross, 2014, 2015, 2016), i.e., the general tendency for more stable,  
108 persistent and unchangeable entities and characters in the system, unambiguously stability-based  
109 sorting (SBS) according to the conception proposed by Vrba and Gould (1986) and Gould (2002, p.  
110 659). This term avoids any connotations that attribute the phenomenon only to material, immaterial,  
111 living or non-living entities, its confusion with natural selection, which we consider a specific  
112 manifestation of this universal principle (see section 2.1), and its confusion with sorting based on any  
113 other kinds of criteria. We will clarify the relationship of SBS and selection more thoroughly in the

114 next section. More particularly, we will show that selection is just one special manifestation of the  
115 general process of SBS (a relationship that was implied by numerous evolutionary-biological scholars  
116 of the role of persistence in nature mentioned above, e.g. Dawkins, 1976, Okasha, 2006, Godfrey-  
117 Smith, 2009, Bouchard, 2011, Doolittle, 2014, or Bourrat, 2014). However, despite being related in  
118 their essence, selection, as a special case of SBS, has markedly different evolutionary consequences.  
119 Therefore, because the aim of this article is predominantly to demonstrate and stress the different  
120 evolutionary consequences of the two processes (deeply understudied SBS in the strict sense and usual  
121 conception, and its special case, selection), we will consider SBS and selection as separate phenomena  
122 from now on.

## 123 2 Results and Discussion

### 124 2.1 The relationship between selection and SBS

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

136 SBS and selection act both in open and growing systems, and in closed systems with a  
137 stagnating number of entities. For example, in the course of a snowstorm, the number of competing  
138 entities (snowflakes) is not limited and will constantly grow in the snow cover (an open system into  
139 which new snowflakes constantly arrive from the system’s surroundings). In such a system, the

140 number of less stable entities will constantly decline, but never reach zero because of the constant  
141 share of unstable variants among newly arriving snowflakes<sup>2</sup>. In a closed system, e.g. during the  
142 evolution of our universe after the Big Bang with a limited amount of matter available to form space  
143 objects, or during memetic evolution of some exclusive religious beliefs that is limited by the number  
144 of members of society, more stable entities will gradually replace less stable entities (space objects or  
145 memes). The same applies to selection. In an open system, e.g. an exponentially growing unlimited  
146 population, the number of individuals better adapted to their environment will gradually grow, but  
147 worse adapted individuals will remain in the system too. In a closed system, e.g. in a chemostat or a  
148 turbidostat (Flegr, 1997), worse adapted individuals with lower speed or effectiveness of reproduction  
149 are quickly displaced by their better adapted counterparts. Thus, in both cases, evolution will proceed  
150 faster in closed systems.

151 In most systems, SBS acquires solely the form of competition among entities for the highest  
152 *static stability*, i.e., lowest probability of expiration or transformation of individual entities or their  
153 traits into something else. In a particular class of systems—those in which new entities originate from  
154 parental entities and inherit their traits—SBS becomes predominantly the competition for the highest  
155 *dynamic stability* (Pross, 2003, 2004, 2012; Wagner and Pross, 2011; Pascal and Pross, 2014, 2015,  
156 2016). The competition of stable coexisting entities for the longest static persistence becomes  
157 competition for the ability to produce the highest number of their own copies (i.e. the copies of the  
158 information how to copy itself), or more precisely, competition for the largest difference between the  
159 speed of generation and expiration of these copies. This difference is based both on the longevity of  
160 entities (e.g. length of the reproductively active life in organisms), as in the case of static stability, and  
161 on the speed of their generation, e.g. reproduction or speciation (*Malthusian kinetics* of Pascal and  
162 Pross, 2014, 2015, 2016; see also Pross, 2003, 2004, 2012, and Bourrat's, 2014, models). Darwin's  
163 natural selection (as well as Dawkins' interallelic competition, Dawkins, 1986, and Vrba's and  
164 Gould's species selection, Vrba and Gould, 1986; Gould, 2002) are thus special cases of general SBS.  
165 Sorting based on dynamic stability (i.e. selection) and sorting based on static stability differ in the

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<sup>2</sup> Dynamics of such a system were modelled, e.g., by Doolittle (2014).

166 nature of what is sorted—entity itself versus the *information* how to create its copies. From a certain  
167 perspective, information emancipates from matter in the case of selection (Shcherbakov, 2012). This  
168 makes us to expect both kinds of sorting to take place in evolution of systems of replicating entities  
169 with heredity, directly affecting its course and perpetually interacting in their effects.

170 This is in full agreement with Bourrat’s (2014) arguments that were supported by numerical  
171 models of the continuous transformation of populations of entities sorted purely on the basis of static  
172 stability to populations of genuine replicators. Similar views were presented even earlier, see e.g.  
173 Slobodkin and Rapoport (1974), Rappaport (1999), Bouchard (2008, 2011) or Bardeen (2009). Pross  
174 (2003, 2004, 2012), Wagner and Pross (2011) and Pascal and Pross (2014, 2015, 2016 and references  
175 therein) studied the role of stability in nature from another angle, differentiating physical forces  
176 standing behind stability kinds. Their concept and terminology, however, differ in some important  
177 details from the presented one (see Fig. 1 and Appendix).

178 In the case that selection, not only SBS in its strict sense, affects the evolution of a certain  
179 population; entities that do not invest in their maintenance (and thus have low longevity) but channel  
180 the majority of their resources to reproduction may easily prevail. Selection thus represents sorting  
181 based on dynamic stability, i.e., a specific form of SBS in the broad sense, whereas SBS in the strict  
182 sense and its usual conception represents sorting on the basis of static stability. Therefore, we will  
183 respect a traditional terminology, use the term SBS exclusively to refer to sorting on the basis of static  
184 stability, and call sorting on the basis of dynamic stability by its standard term—selection (for a more  
185 radical approach regarding the classification of selection, see e.g. Pross, 2004, 2012). [FIG. 1 HERE]

186 It would be erroneous to consider SBS a process from whose direct influence the entities  
187 undergoing natural selection completely escaped. As Dawkins (1976, p. 13) stressed, this process is in  
188 each sense more general. It acts constantly and simultaneously on all levels. Moreover, the stable  
189 accumulates and unstable vanishes regardless of the origin of sorted entities or the nature of the sorting  
190 process. Shcherbakov (2012, 2013) goes even further and argues on this basis that the inevitable  
191 consequence of every evolution is stasis. Invariance, not variability, is the attractor of evolution.  
192 According to this author, any evolutionary changes are only by-products of evolution, e.g. the inability



193 of organisms to completely avoid mutations, or transient consequences of opportunism of selection-  
194 based evolution manifested by transient predominance of entities that are less stable in the long-term  
195 but have higher dynamic stability—higher fitness—in the short-term. This conclusion might seem  
196 quite extravagant taking into account all the variability of life forms on Earth. However, it is the  
197 logical consequence of the appreciation of the role of SBS in evolution. It is also worthy to note that  
198 Wagner and Pross (2011) and Pross (2012) take the opposite stand, reducing the role of static  
199 thermodynamic stability (see Appendix) in the systems of replicating entities only to a general  
200 constraint and postulating their general tendency to complexify.

201           Contrary to both of these approaches, we believe that the role of SBS in the systems of  
202 replicating entities with heredity is direct but subtle and selection is rather its tool than by-product,  
203 which was suggested only implicitly by Shcherbakov (2012)<sup>3</sup>. In a simple case (stable and  
204 homogenous environment), entities in the system would compete only for the highest number and  
205 accuracy of copies, i.e., the speed of reproduction associated with its precision, achieved, for example,  
206 by reduction of genomic size (which is also the outcome of numerous computer simulations of  
207 biological evolution, see e.g. Ray 1993, 1997; Thearling and Ray, 1994, 1996, or Ray and Hart, 1998,  
208 as well as experiments, see e.g. Mills et al., 1967). In the real world, the entities are affected by much  
209 more heterogeneous conditions of the environment, including other co-evolving entities that undergo  
210 selection and mutually interact in a very complex manner. The outcome is constant tension between  
211 the pressure to conserve information (i.e., to increase the speed and precision of reproduction) and its  
212 evolution (i.e., adaptation to new conditions). Entities that reproduce most rapidly and precisely are  
213 not necessarily most successful under these conditions. The increased persistence of individual entities  
214 remains the ultimate attractor, yet not by trivial means (static persistence or speed of reproduction), but  
215 through more sophisticated adaptations. From our point of view, evolvability is not a mere by-product  
216 of evolution. It is an important meta-adaptation that enables an actual increase in the persistence of  
217 entities in the process of sorting on the basis of dynamic stability—selection.

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<sup>3</sup>           “Evolution is resistance to entropy, the adaptation to environment being only one of the means of this resistance.”

218           Moreover, in the case of terrestrial life, the selected information, which was originally coded  
219 directly in the replicating sequence of nucleotides, emancipated to some degree from its material basis.  
220 Replicators evolved interactors—bodies—that interpret the information embedded in the sequence of  
221 nucleotides in various context-dependent ways. These interactors started new rounds of competition  
222 on higher levels, so that the meaning or interpretation of genetic information and the DNA–body  
223 complex became the subject of selection rather than the nucleotide sequence itself (Markoš, 2002;  
224 Ostdiek, 2011; Shcherbakov, 2012). The consequence is that interacting entities themselves  
225 (replicators), as well as the replicated information, change in the course of evolution but still maintain  
226 their historical individuality. The outcome of any such competition can be estimated with the help of  
227 game theory, particularly the theory of evolutionarily stable strategies (Maynard Smith and Price,  
228 1973; Kolokoltsov and Malafeyev, 2010, p. 65), and if the whole system is complex enough (as e.g.  
229 the terrestrial biosphere), it need not immediately follow the path to evolutionary stasis. This,  
230 however, does not contradict the SBS-mediated accumulation of stable entities that resist selective  
231 pressures and have decreased evolvability; it continuously proceeds on all levels regardless of the  
232 effects of selection. The course of evolution on the largest scale can thus be seen as a constant struggle  
233 between stability or conservation on one side, and adaptation on the other, which, as will be shown in  
234 section 3, can have interesting evolutionary consequences.

## 235 2.2 Differences between selection and SBS

236           SBS is much more widespread than natural selection and probably takes place in all evolving  
237 systems (i.e., systems with memory/history) with the exception of closed systems with a fixed  
238 maximum number of entities in which it proceeded completely, i.e., where only absolutely stable non-  
239 expiring entities that are incapable of any change accumulated and remained. In selection, the most  
240 successful entities are those that produce the most offspring until their expiration, i.e., death. In SBS,  
241 the most successful entities are the most stable ones—those that persist for the longest time without  
242 expiring or changing into something else. Selection is much more efficient. Ensuring that offspring  
243 inherit the traits of their parents and that the speed of offspring production is based on the number of  
244 beneficial traits of the individual, selection gradually accumulates and amplifies beneficial traits,

245 which give individuals a higher dynamic stability—higher fitness. Thus, more (on average) better-  
246 adapted individuals and fewer worse-adapted individuals are produced in time. This pattern may be  
247 partially masked by the Red Queen effect (Van Valen, 1973). Competitors, predators and parasites  
248 evolve counter-adaptations so that, for example, the final speed or effectiveness of reproduction of  
249 members of a certain population or species seemingly stagnates until we artificially prevent the  
250 counter-evolving species to respond to evolutionary moves of the studied species (see e.g. Becerra et  
251 al., 1999). On the other hand, the same share of stable and unstable entities (e.g. snowflakes) originate  
252 in the course of SBS regardless of the previous evolution of the system, and especially regardless of  
253 the average stability of entities currently constituting the system. This does not fully apply to some  
254 memes. For example, new ideas are created with regard to past ones and authors of new ideas  
255 preferentially generate such that they have a higher chance of success in long-term competition with  
256 existing ones (a process analogical to “copy-the-product”, see Blackmore, 1999, pp. 59-62). However,  
257 this is probably specific to entities created by conscious beings that are able to (at least partially)  
258 anticipate future development of the system (see e.g. Blackmore, 1999).

259         In the course of the evolution of a certain genealogical lineage, incomparably more complex  
260 adaptations originate by means of the gradual accumulation of mostly small changes (beneficial  
261 mutations) in natural selection than by means of much more widespread SBS. It is clear that random  
262 changes that increase the stability (persistence) of entities may also accumulate in systems without  
263 selection, but this process would be incomparably less effective and slower (see Bourrat, 2014).  
264 However, it is possible in principle, as was modelled by Doolittle (2014). In the course of selection in  
265 closed systems (which are, in the long term, all systems undergoing biological evolution), every  
266 beneficial change spreads to most or even all members of the population. Newly originated beneficial  
267 change thus would almost always affect the individuals that already bear the previous one. In SBS, the  
268 probability of a simultaneous occurrence of several changes that increase the stability of one newly  
269 originated individual is negligible, and the time necessary for the accumulation of a larger number of  
270 changes that are beneficial in terms of stability in one individual might be incomparably longer than its  
271 estimated lifespan (see Bourrat, 2014). For example, the chamber eye evolved multiple times

272 independently by means of natural selection (Fernald, 2000). It is, however, very unlikely that such a  
273 complex organ would evolve solely by means of SBS.

274 In spite of lower efficiency of SBS, a certain category of adaptations that we see in modern  
275 organisms probably originated by means of SBS rather than selection. However, these can only be  
276 characters that originated by one or two changes, not a long chain of consequential changes that would  
277 continuously elaborate a certain function. An important source of adaptations that increase the stability  
278 of sorted entities (e.g. individuals in natural, i.e. intraspecific, selection or evolutionary lineages in  
279 species selection) are preadaptations. Such characters evolved by means of selection as adaptations to  
280 a certain function, but later turned out to be advantageous in terms of stability and thus spread and  
281 prevailed by the means of SBS. SBS works as a sieve that selects characters contributing to the long-  
282 term stability of entities that constitute the system and also the system itself (Doolittle, 2014). An  
283 example of such a character may be obligate sexuality (Davison, 1998; Flegr, 2008, 2010, 2013;  
284 Shcherbakov, 2010, 2012, 2013; Gorelick and Heng, 2011), which originated by natural selection,  
285 likely as one of the mechanisms of reparation of mutations, especially structural damage to DNA  
286 (Bernstein and Bernstein, 2013; Hörandl, 2013)<sup>4</sup>. Only *ex post* did it turn out that sexuality  
287 significantly contributes to the stability of its holders—sexual species—in heterogeneous, changeable  
288 and often unpredictable conditions ruling on most of the Earth’s surface. Asexual species are  
289 constantly at risk of adapting to temporarily changed conditions, losing their genetic polymorphism  
290 and not being capable of re-adaptation to original (or any other) conditions fast enough. This could  
291 even lead to their extinction. Sexual species, on the other hand, adapt to transient environmental  
292 changes only imperfectly, and constantly maintain high genetic polymorphism (including currently  
293 disadvantageous alleles) because of the effects of genetic epistasis and pleiotropy in conjunction with  
294 frequency dependent selection. Therefore, they are always able to quickly re-adapt by the changes of  
295 allelic frequency (Williams, 1975, pp. 145-146, 149-154, 169; Flegr, 2008, 2010, 2013). From the

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<sup>4</sup> The so called “reparation theories” are only one of many concepts proposed for the origin of sexual reproduction. See e.g. Birdsell and Wills (2003) for other proposed theories of the origin of sexual reproduction. However, the vast majority of them assumes that original purpose of sexual reproduction and the reasons of its subsequent spread and long-term maintenance differ.

296 perspective of individual selection, sexuality is, accompanied by the two-fold cost of meiosis, two-fold  
297 cost of sex and other handicaps of its holders (Lehtonen et al., 2012), disadvantageous. From the  
298 perspective of species selection—in this case the lower probability of extinction of species in  
299 heterogeneous environment—it is highly advantageous. However, species selection is weaker and  
300 cannot act against individual one. From the perspective of SBS, it is highly advantageous as well;  
301 species and lineages that reverse to asexual reproduction are sorted out, i.e., perish, those that cannot  
302 reverse to asexual reproduction for any reason accumulate, and by this mechanism sexuality might  
303 spread and prevail.

304 SBS cannot gradually generate such spectacular adaptations as, e.g., chamber eye, yet it  
305 always has the final word in evolution and is even able to completely reverse the course of evolution  
306 driven mostly by selection. For example, the human brain and consciousness are undeniably one of the  
307 most remarkable characters among terrestrial organisms. However, it is possible that this brain that  
308 enabled humans to dominate the Earth and establish a multi-billion population may also be the reason  
309 of our early extinction, either by the means of catastrophic warfare, failed physical or biological  
310 experiment or “prosaic” severe viral infection that could spread only in a sufficiently dense and  
311 interconnected population. From the macroevolutionary point of view, humans may be easily outlived  
312 by species in which some ontogenetic constraints in the role of preadaptation prevented the evolution  
313 of a sufficiently efficient brain.

314 Selection is opportunistic. It would beat seemingly “forward planning” SBS in a stable  
315 environment (see e.g. Ray, 1993, 1997; Thearling and Ray, 1994, 1996; Ray and Hart, 1998).  
316 However, in a changing environment, i.e., under the realistic conditions of Earth’s surface, it is  
317 otherwise. Selection does not “plan in advance” and thus is only able to improve the adaptation of  
318 organisms on the current conditions regardless of the risk of impairing their future chances of survival,  
319 including the risk of extinction of the whole species. Considering the “adaptive landscape” (Wright,  
320 1932), species and populations are able to move only in the upward direction under normal conditions  
321 and thus are able to occupy only local, not global, optima. Descending a little and then ascending on  
322 another slope for the occupation of a higher peak in the adaptive landscape would not be possible

323 under the normal regime of selection. Mutants that descend have lower fitness and they or their  
324 offspring are removed from the population before accumulating other mutations, reaching the “bottom  
325 of the valley” and starting to ascend on another slope. On the other hand, SBS does not have such a  
326 limitation and is subject to much less opportunism<sup>5</sup>. In the case that a certain adaptation (e.g. a certain  
327 pattern of altruistic behaviour) decreases the chance of survival of an individual or slows down its  
328 reproduction, yet simultaneously enhances the chances of survival of the population of the individual’s  
329 species, those (probably rare) populations and species in which the adaptation prevailed would prosper  
330 and survive in the long term.

331 In most species and within them in most populations, individual selection would act against  
332 these tendencies and prefer mutants that lose the individually disadvantageous character. However,  
333 populations and species that are preadapted with safeguards against such reverse changes would  
334 prevail in the end. Returning to the previous example, such safeguard against the reversal of asexual  
335 reproduction may be for example mammalian genomic imprinting that significantly reduces the  
336 chance of successful transition to asexual reproduction (Bartolomei and Tilghman, 1997). This and all  
337 similar safeguards originated as preadaptations, i.e., adaptations for another purpose, or as spandrels,  
338 i.e., characters without any function formed purely as the consequence of topological, physical,  
339 biochemical or ontogenetic constraints (see e.g. Gould, 2002). Many species presumably did not have  
340 any such safeguards, but we don’t see them today because they lost to their counterparts in the process  
341 of SBS. Rare extremes are usually more important than average values both in intraspecific and  
342 interspecific evolution (see e.g. Dobzhansky, 1964, or Williams, 1975). Winner usually “takes all”.  
343 The fact that the vast majority of populations do not have safeguards and are dominated by selfish  
344 individuals means nothing if a safeguard is present in at least some populations. It would be the  
345 populations that bear the safeguard that would determine the evolution of a studied species. Similarly,

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<sup>5</sup> A certain degree of opportunism can manifest only in SBS ongoing in a closed system. Stable entities that are resistant to current effects of environment, or effects that do not actually affect the system but happen relatively often, could prevail there. In closed systems, this precludes the occurrence of entities that would be more resistant to another, possibly much stronger, effect of environment that happens much less often. On the other hand, SBS ongoing in open systems is not opportunistic at all. Ultimately stable entities always prevail there in the long term.

346 if there happens to be a safeguard against the loss of sexuality or altruistic behaviour in certain species  
347 that is absent in the vast majority of others, we will meet only the species with such a safeguard and  
348 their descendants in the long term.

### 349 3 General Discussion

#### 350 3.1 Phenomena in which SBS plays an important role

##### 351 3.1.1 Microevolutionary phenomena

352 SBS is much more widespread than selection. However, in the reign of biological evolution,  
353 and especially in the processes operating on the human (ecological to microevolutionary) timescale, its  
354 significance is obscured by spectacularly manifesting natural selection. SBS is thus encountered  
355 especially in phenomena whose origin, establishment or maintenance wasn't convincingly explained  
356 by natural selection yet. Such products of SBS may be, for example, sexuality mentioned in section  
357 2.2 or some types of altruistic behaviour, including restrictions on individual reproduction under the  
358 risk of overpopulation that were widely discussed in the past (Dawkins, 1976; Wilson, 1983; Wynne-  
359 Edwards, 1986; Leigh, 2010). The usual assumption is that individuals that "voluntarily" reduce the  
360 speed of their reproduction would be displaced by selfish mutants (i.e., eliminated by selection). The  
361 whole phenomenon is interpreted not as an evolutionary adaptation that increases the long-term  
362 success of populations, but as an individual adaptation that enables the individual to save its resources  
363 in the situation of high offspring mortality. The proximate reasons for this phenomenon are also being  
364 emphasized, e.g. territoriality, social hierarchy, or that individuals in too dense a population disturb  
365 each other, reducing the success of each other's reproduction (Wynne-Edwards, 1986). However,  
366 these proximate reasons may act as the safeguards described in section 2.2 that enables certain  
367 populations not to be dominated by selfish individuals, which are able to reproduce regardless of the  
368 risk of overpopulation. The existence of a safeguard, e.g. the population density-dependent ability "to  
369 be disturbed" by nearby individuals, might give the species a chance to overcome the risks of fatal  
370 overpopulation and thus give it the decisive advantage in SBS. Species without this or some similar  
371 safeguard were more susceptible to extinction and thus we do not meet them today.

372 Doolittle (2014) suggested that another product of the process that we call SBS may be  
373 widespread and often intensive horizontal gene transfer (HGT). According to this author, it may  
374 significantly accelerate the adaptations of (especially prokaryotic) organisms to environmental  
375 stressors. Such acceleration is probably advantageous in two ways: in terms of individual selection in  
376 the short to medium-term and, as will be shown in section 3.1.3, in the long-term because of the  
377 gradual stabilisation of environmental conditions (Markoš, 1995; Doolittle, 2014). In a similar way to  
378 sexual reproduction mentioned in section 2.2, the original purpose of HGT was probably completely  
379 different (it probably served for horizontal spread of selfish genetic elements, see e.g. Redfield, 2001).  
380 However, species and lineages that evolved safeguards against the loss of ability to undergo HGTs  
381 preserved the ability of relatively fast reactions to the changes of conditions. The most profound  
382 safeguard against the loss of HGT ability may be the extraordinary conservation of genetic code  
383 (Markoš, 1995; Syvanen, 2002; McInerney et al., 2011)—evolutionary lineages that deviated too  
384 much and compromised their ability to undergo HGTs were sorted out by lineages that could still  
385 enjoy its benefits.

386 Similarly, SBS can explain the wide distribution of certain strikingly restrictive traits of  
387 modern organisms, i.e., safeguards against the loss of a trait that is beneficial in the long-term. Some  
388 examples might be e.g. genomic imprinting of mammals mentioned in section 2.2 or a similar  
389 phenomenon in gymnosperms, whose embryos require organelles from the paternal gamete for  
390 successful development (Neale et al., 1989); or the extraordinary conservation of genetic code that  
391 may enable mutual compatibility of organisms in horizontal gene transfers (Markoš, 1995; Syvanen,  
392 2002; McInerney et al., 2011).

### 393 3.1.2 Macroevolutionary phenomena

394 SBS may also explain certain macroevolutionary phenomena. It is probably tightly connected  
395 to the phenomenon of evolutionary stasis, or the punctuated pattern of evolution of (especially) sexual  
396 organisms (see e.g. Eldredge and Gould, 1972, or Gould, 2002, pp. 745-1024, with particular  
397 examples on pp. 822-874). As was already mentioned, sexual reproduction spread and is still  
398 maintained by means of SBS—it helps to maintain high genetic polymorphism, prevents opportunistic



399 one-way adaptation accompanied by loss of genetic polymorphism and enables fast and reversible  
400 evolutionary reactions to fluctuations of conditions in changeable and heterogeneous environments by  
401 means of epistasis and pleiotropy interconnected with frequency-dependent selection (Flegr, 2008,  
402 2010, 2013). Another consequence of SBS in sexual species is the accumulation of functionally  
403 interconnected alleles on the level of an individual and a population. Alleles that are tightly and non-  
404 trivially interconnected in their effects on a phenotype, especially alleles that are maintained in a  
405 polymorphic state by frequency-dependent selection, are extremely hard to fixate or eliminate through  
406 any type of selection and thus are more persistent and accumulate in populations (Flegr, 2008, 2010,  
407 2013). Such “microevolutionary freezing” may be beneficial even to individual organisms—for  
408 example, it may enhance the robustness of development to internal and external changes  
409 (Shcherbakov, 2012). Sexual species thus remain in evolutionary stasis for most of their existence and  
410 are able to irreversibly change only under certain conditions, as was suggested by Eldredge and  
411 Gould (1972)<sup>6</sup>. This is in accordance with Sheldon’s (1996) theory *Plus ça change* that highlights the  
412 difference between paleobiological evolutionary patterns of species of changeable environments  
413 (punctuated evolution) and species of stable environments (gradual evolution). The difference between  
414 these “generalists and specialists in geological timescale” may stem from the presence, or absence, of  
415 sexual reproduction.

416         The very prominent and almost universal pattern of macroevolutionary processes is also a  
417 non-monotonous change in disparity, i.e., morphological and functional variability (e.g. in the number  
418 of body plans), in the course of the evolution of particular evolutionary lineages, or more precisely,  
419 particular taxa. Every clade of an evolutionary tree originates in a speciation event and initially  
420 contains a single species. Thus, it has minimal diversity (number of species) and minimal disparity at  
421 the beginning. The number of species and morphological and functional diversity then grow in the

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<sup>6</sup> Several alternative hypotheses for the conditions under which species in the state of evolutionary stasis may start to irreversibly respond on selective pressures were suggested already by Eldredge and Gould (1972). However, the transition between the “plastic” and “elastic” phase of the species’ evolution is probably most thoroughly described by Frozen Plasticity Theory, see e.g. Flegr (1998, 2008, 2010). All types of punctuationalistic theories of evolution and proposed conditions for the above-mentioned transition were comprehensively summarized by Flegr (2013).

422 course of the evolution of a lineage, as do the number of different phenotypically distinct clades and  
423 number of higher taxa described by paleontonomists within the original evolutionary lineage.  
424 However, individual sub-clades die off in time and only clades whose species differ in continuously  
425 decreasing number of still less essential traits originate within the remaining clades. The number of  
426 species of the original taxon, diversity, need not necessarily decrease and may even grow for a  
427 considerable time. Its disparity, on the other hand, decreases (Rasnicyn, 2005; Erwin, 2007; Hughes et  
428 al., 2013). According to the class of developmental explanations of this phenomenon, the taxon  
429 exhibits high evolvability, i.e., “evolutionary plasticity”, at the beginning. Its members can initially  
430 change in almost every trait under appropriate selective pressures. In time, more and more traits  
431 “macroevolutionarily freeze”, so that modern members of the taxon are not able to evolve such  
432 profoundly new adaptations and lifeforms that were evolved by the species in earlier stages of the  
433 evolution of the clade (Foote, 1997; Eble, 1998; Erwin, 2007). The taxon thus gradually abandons  
434 different parts of morphospace and perhaps only one, often very specialized and phenotypically very  
435 uniform, clade survives at the end. For example, only the species-rich but morphologically rather  
436 uniform clade of birds (Aves) survived from original highly disparate clade of dinosaurs to the present  
437 (Chiappe, 2009). An even more extreme example of gradual loss of disparity, which is in the long-  
438 term probably accompanied by the loss of diversity because of decreasing evolvability, may be the so-  
439 called “living fossils” (see e.g. Lloyd et al., 2012). The phenomenon of dead clade walking (Jablonski,  
440 2002), i.e., higher susceptibility to extinction in many isolated lineages of higher taxa that survived  
441 mass extinction, may also be a manifestation of the same process. It is probable that these lineages are  
442 macroevolutionarily frozen and their possible responses to selective pressures of the post-extinction  
443 environment are thus very limited.

444         A spectacular example of macroevolutionary freezing is the evolution of multicellular animals.  
445 The common ancestor of all bilaterians lived approximately 700 million years ago, whereas the  
446 common ancestor of all metazoans probably did not precede them by more than 100–200 million years  
447 (Douzery et al., 2004; Peterson et al., 2008; Erwin et al., 2011). However, metazoans did not exhibit  
448 any significant diagnostic characters until Cambrian or at least Ediacaran, and they probably consisted

449 of mm-sized creatures without hard parts that would enable their identification and classification in  
450 fossil material. However, something happened in the early Cambrian approximately 540 million years  
451 ago, and metazoans started evolving rapidly and differentiating into many morphologically and  
452 ecologically distinct forms, future metazoan phyla (Shu, 2008). This initial period was short and lasted  
453 tens of millions of years maximally (Erwin et al., 2011). All current animal phyla, and several tens of  
454 other phyla that gradually died out in the next millions of years, originated during this time (Gould,  
455 1989). No other animal phylum and, with the exception of certain groups of radically simplified  
456 parasitic organisms (Canning et al., 2004; Glenner and Hebsgaard, 2006; Murchison, 2008), no  
457 radically new body plans have originated since the end of the Cambrian. The trend of a gradual  
458 decrease of disparity in the course of the evolution of a lineage was also documented in many  
459 particular taxa of multicellular animals and plants (Erwin et al., 1987; DiMichele and Bateman, 1996;  
460 Eble, 1999). Other examples were summarized by Gould (1989) or Erwin (2007), and, according to  
461 Hughes et al. (2013), this trend is characteristic for Phanerozoic clades of metazoans in general.  
462 Particular macroevolutionary frozen traits are, for example, the patterns of head segmentation  
463 characteristic of main groups of arthropods, five-fingered legs of tetrapods, or (with a few exceptions)  
464 seven cervical vertebrae of mammals. All these currently frozen traits were, in some cases even  
465 considerably, changeable in the early stages of the evolution of respective taxa (Hughes et al., 2013).

466         The gradual macroevolutionary freezing of individual traits is almost certainly not just  
467 taxonomic artefact caused by the subjectivity of our view from the recent perspective and the way  
468 paleotaxonomists delimit taxa of higher and lower level (older combinations of characters delimit  
469 higher taxa and *vice versa*). Freezing of individual traits in the course of macroevolution is a real  
470 phenomenon that is observed even on the intraspecific level. On this level, it was first described by  
471 Italian zoologist Daniele Rosa, and is known as Rosa's rule today (Rosa, 1899). For example,  
472 intraspecific variability of particular morphological characters and the number of characters in which  
473 this variability is exhibited are much greater in the early branched-off species than in later branched-  
474 off species of certain taxon. Particular evidence for this pattern is the gradual decrease of intraspecific  
475 variability in trilobites (Trilobita). Webster (2007) documented that the relative proportion of species

476 with at least one intraspecifically polymorphic morphological character decreased from 75% in middle  
477 Cambrian to 8% in late Cambrian. After the subsequent rise to 40% in early Ordovician, it just more or  
478 less monotonically decreased until middle Devonian. At that time, the intraspecific polymorphism  
479 vanished completely, not to show again until the extinction of taxon at the end of Permian. The  
480 temporal pattern in proportion of characters coded as intraspecifically polymorphic is even more  
481 striking, declining from a median of 2,8% and 3,6% in middle and late Cambrian to a median of 0% in  
482 post-Cambrian. The primary reason for the freezing of individual characters in the course of  
483 macroevolution is therefore most likely the freezing of these characters within particular species. If  
484 species cease to vary in certain trait, there are no diverse variants of this trait among which selection  
485 might differentiate. Such species are thus unable to adapt to conditions to which species cleaved early  
486 in the evolution of respective taxon were able to adapt easily (Webster, 2007).

487         Frozen Evolution Theory (do not confuse with Frozen Plasticity Theory which describes the  
488 causes of alternation of short “evolutionarily plastic” and long “evolutionarily elastic” phases in  
489 species’ lifetimes) assumes that the reason for the macroevolutionary freezing of individual traits and,  
490 consequently, taxa (monophyletic sections of the evolutionary tree delimited by a taxonomist on the  
491 basis of a unique combination of several diagnostic characters) of sexual organisms is SBS (Flegr,  
492 2008, 2010, 2013). Various characters exhibit various degrees of evolvability, i.e., the ability to  
493 change under appropriate selective pressures, given by the way of their genotype–phenotype mapping  
494 and frequency-dependent effect on fitness (Flegr, 2008, 2010, 2013). In the initial phase of the  
495 evolution of a certain taxon, a large part of the characters of its members are easily changeable, a  
496 smaller part harder and only a small fraction, probably those that the members of the taxon inherited  
497 from their evolutionary ancestors, not at all or to a very limited extent. Individual characters change in  
498 the course of the taxon’s evolution, even in terms of their variability and evolvability. Traits that are  
499 able to change easily and distinctly under proper selective pressures appear and disappear, whereas  
500 stable traits persist and accumulate in the taxon. More and more traits irreversibly freeze by means of  
501 this sorting, both on the intraspecific and interspecific level. Intraspecific variability is decreasing in a  
502 growing fraction of traits. The disparity of the whole taxon is decreasing because old evolutionary

503 lineages of the taxon slowly die out and newly originating species can be distinguished from the  
504 original species only to a limited degree in a small and constantly decreasing number of traits.

505           Organisms, or their evolutionary lineages, may theoretically avoid irreversible  
506 macroevolutionary freezing through species selection (Stanley, 1979). Competition for the highest rate  
507 of speciation and lowest rate of extinction should theoretically ensure that the lineages with the highest  
508 (remaining) evolvability prevail in the long-term. However, SBS, whose manifestation is also  
509 macroevolutionary freezing, probably cannot be reversed by species selection, i.e., sorting on the basis  
510 of dynamic stability at the species level. Irreversible macroevolutionary freezing is a ratchet-like  
511 process that continuously accumulates stable characters and traits in all lineages simultaneously. It  
512 cannot be ruled out that certain new species may rarely acquire a unique combination of characters  
513 that was not sorted on the basis of stability yet, which would probably mostly accompany its transition  
514 to a completely different environment or the adoption of a new ecological strategy. A certain  
515 seemingly irreversibly frozen character, or combination of characters, may also exceptionally “thaw”  
516 in the course of the evolution of a lineage and start to respond to selection again. Both these events  
517 might stand on the beginning of the evolution of birds whose common ancestor conjoined several  
518 unique adaptations (Brusatte et al., 2014) and uncoupled the development of front and rear legs to a  
519 considerable degree (Dececchi and Larsson, 2013). However, a more fundamental thaw, e.g. thawing  
520 of whole body plan, is probably extremely rare, and if it happens, it has the character of a radical  
521 simplification of current individual development. This can be demonstrated, e.g., on the example of  
522 endoparasitic crustaceans from the clade Rhizocephalia (Glennner and Hebsgaard, 2006), seemingly  
523 unicellular endoparasitic cnidarians from the clade Myxozoa (Canning et al., 2004) or sexually- or  
524 biting-transmitted mammalian cancers (Murchison, 2008). These radically simplified species may  
525 become founders of entirely new, initially macroevolutionary very plastic, but gradually irreversibly  
526 freezing high-ranking taxon.

### 527 3.1.3 Ecological and geophysiological phenomena

528           SBS acts even on the ecosystem level, and, in the largest spatial and temporal scale, on the  
529 level of the whole planet. Communities in a newly establishing ecosystem (e.g. after severe fire,

530 deglaciation, or emersion of a new island) undergo ecological succession. With a certain degree of  
531 simplification, ecosystems are heading towards an equilibrium state—climax—in which they can stay,  
532 or around which they can oscillate, for a considerable time in the absence of significant changes to  
533 environmental conditions (see e.g. Walker and del Moral, 2003)<sup>7</sup>. The development of communities  
534 towards the stage of climax is of various lengths and complications and the final climax communities  
535 may vary according to the character of disturbances, amount of available resources and energy etc. (in  
536 other words, a climax community may be a polar growth of lichens, as well as a tropical rainforest).  
537 Ecological succession is a multidimensional process and takes place on many levels. It may even lead  
538 to significant changes in abiotic conditions of the environment. However, it always follows the rules  
539 of SBS. Individual species are sorted based on their persistence in the context of a dynamically  
540 changing community. An important component of this persistence is their current ecological success.  
541 In the long-term, however, their contribution to the stability of the ecosystem is much more important  
542 (Bardeen, 2009). This contribution need not be active and need not be paid at the expense of  
543 individual fitness (such a system could be extremely easily invaded by selfish entities). It is, rather,  
544 based on the species' ecosystem function, its by-products and side effects—safeguards on the  
545 ecosystem level. Species that unidirectionally change the environment towards the conditions  
546 suboptimal for them disappear, whereas species that are incorporated in various negative feedback  
547 loops that maintain conditions favourable for them persist. Thus, an ecosystem at an advanced stage of  
548 development is usually able to compensate (at least to some degree) for the effects of biotic and abiotic  
549 environments that lead it off current balance. However, if the intensity of these effects exceeds a  
550 certain threshold, the ecosystem may, sometimes profoundly, change (e.g. after distortion of the  
551 ecosystem by an invasive species, or change in the soil pH caused by certain tree species). Such  
552 change leads to further change in the course of ecological succession (Walker and del Moral, 2003).

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<sup>7</sup> Taking into account the plethora of factors of biotic and abiotic environments that affect terrestrial organisms, it is better to consider the concept of climax as depicted here a simplification; a mobile attractor at best, towards which all ecosystems are usually heading but almost never reach. This, however, does not contradict the general tendency of ecosystems to evolve towards a stable climax stage, i.e., the accumulation of species that maintain stable conditions for their survival in the context of other biotic and abiotic factors.

553 Certain changes may be destructive—exceptional cases even on the global scale—e.g. the origin of  
554 oxygenic photosynthesis that completely altered global conditions on Earth. Such events are described  
555 by the Medea hypothesis, see Ward (2009). However, Medea-class events are probably very rare and  
556 organisms are thus able to adapt to the resulting changes with the help of selection on the evolutionary  
557 timescale. On the other hand, if the changes exceed a critical threshold, or if they are too fast (this  
558 applies more to the catastrophic events of abiotic character, e.g. the impact of large cosmic bodies),  
559 they can lead to the extinction of all (at least surface) life on the planet.

560         The strong version of the Gaia hypothesis (Lovelock, 1979) was rejected by most evolutionary  
561 biologists because of its assumption that planet Earth (with the help of terrestrial organisms) actively  
562 maintains conditions suitable for life. According to the hypothesis, this “planetary homeostasis” is  
563 ensured by a broad array of negative-feedback cycles of chemical elements and energy and Earth thus  
564 shows signs of a superorganism. The main argument against it is that the only known possible natural  
565 origin of such a purposeful system involves natural selection (Doolittle, 1981; Dawkins, 1982; Gould,  
566 1988). However, the group selection on behalf of a whole biosphere postulated by Lovelock would  
567 collapse under the pressure of individual selection favouring selfish individuals. The same is true for  
568 species selection. The only other alternative, selection on even higher level—the level of whole  
569 planets or biospheres—is impossible for one non-reproducing and non-competing individual (the  
570 Earth).

571         Nevertheless, such a long-term stable system integrated by negative feedback loops might  
572 develop through sorting of individual geological, atmospheric and biological entities and processes on  
573 the basis of stability, i.e., their contribution to the long-term stability of the terrestrial environment.  
574 This contribution is possible to estimate with the help of game theory, or more specifically, the theory  
575 of evolutionarily stable strategies (Maynard Smith and Price, 1973; Bardeen, 2009; Kolokoltsov and  
576 Malafeyev, 2010, p. 65). Entities and processes that did not contribute to the stability of the system or  
577 directly led it out of balance acted only temporarily, whereas the ones that supported the long-term  
578 maintenance of stability in the context of other forces accumulated. The main difference from  
579 ecological succession mentioned earlier in this section, besides the role of biogeochemical cycles that

580 manifest themselves only on higher spatial and temporal scales, is that it operates on evolutionary, not  
581 ecological, timescales and new biological entities enter the system through speciations, not  
582 colonizations. In a similar way to ecological succession, entities and processes acting against the  
583 establishment of homeostasis might (even substantially) change conditions in the system.  
584 Nevertheless, the general SBS-mediated tendency of the system to develop towards higher stability via  
585 the accumulation of contextually stable elements affects it all the time, on all levels. The later the  
586 system is observed, the more long-term stability supporting entities and processes it accumulates and  
587 thus remains in stable states for longer periods (Doolittle, 2014). This agrees with the observed  
588 decrease in extinction and speciation rates (Raup and Sepkoski, 1982; Gilinsky and Bambach, 1987;  
589 Gilinsky, 1994; Benton, 1995; Alroy, 2008) and accumulation of long-lived genera in the terrestrial  
590 biosphere during the Phanerozoic (Rohde and Muller, 2005). Decreasing sensitivity of the ecosystem  
591 to the effects of newly arriving species was also observed in certain computer simulations, see e.g.  
592 Post and Pimm (1983). Another consequence of SBS is that it is more probable that any such system  
593 (Earth, certain exoplanet etc.) will be met in a long-term stable state than in an ephemeral unstable  
594 one.

595 SBS acts on any space body, even lifeless ones, and always leads to the most stable states  
596 under current circumstances. The equilibrium among geological, geochemical and atmospheric  
597 processes need not be static even on lifeless bodies; it could be dynamic, as was observed, e.g., on  
598 Venus or Titan, and continuously evolve in relation to changes of outer and inner conditions.  
599 However, only in the case when biological entities with a significant effect on the conditions of the  
600 environment take part in this sorting, the whole system is heading towards the long-term stable and  
601 negative-feedback-regulated conditions favourable for this specific class of entities. The establishment  
602 of biogeochemical cycles (planetary homeostasis) is probably further facilitated by the multilevel  
603 character of the sorting of biological entities based on their contribution to long-term stability—they  
604 are sorted on all levels simultaneously including the global level. SBS is thus able to explain the  
605 accumulation of biological entities and processes that maintain conditions suitable for their own  
606 survival with the help of negative-feedback processes without greater difficulties. As in the preceding



607 examples, we should not be surprised that, *ex post*, the whole system looks strikingly non-  
608 evolutionary, almost like it was planned. This is the common feature of systems evolved by SBS.

609 Doolittle (2014) and Bardeen (2009) reached similar conclusions regarding the possibilities of  
610 establishing Gaian planetary homeostasis; they also postulated the evolution of a system (Earth)  
611 towards more stable states through the accumulation of contextually stable elements. Both these  
612 researchers supported their arguments by computer simulations: selection of non-replicating non-  
613 competing entities in the first case and Gaian “daisyworlds” in the second. Doolittle (2014) got  
614 especially close to our conception of SBS. According to this author, classical adaptations do not  
615 originate in this process. It can, however, sort adaptations that originated by means of natural  
616 selection. These adaptations thus serve as mutations of a higher level. Bardeen (2009) elaborates the  
617 basic idea even further and proves that persistence, i.e., long-term stability, is *de facto* the true fitness.  
618 Similar reasoning also lies behind proposals to define fitness as the rate of actual or potential  
619 persistence of biological entities (in Bouchard’s words “differential survival through a time of a  
620 lineage”) in the context of a system (Bouchard, 2008, 2011). However, this is (at least to a high  
621 degree) a direct implication of an even older theory of evolutionarily stable strategies. According to  
622 this theory, organisms compete for the highest persistence, or the continuing in an “existential game”  
623 (Slobodkin and Rapoport, 1974).

#### 624 3.1.4 Cultural and other phenomena

625 SBS-based explanations may be naturally applied even in many non-biological fields that deal  
626 with evolving systems. The principle of SBS was described and used as an explanation for numerous  
627 phenomena e.g. in the fields of artificial intelligence (Slotine, 1994; Runarsson and Jonsson, 1999),  
628 cybernetics (Slotine and Lohmiller, 2001; Slotine, 2003), and even cosmology (Safuta, 2011). Its role  
629 is probably even more significant in cultural evolution. SBS is able, e.g., to explain the continuous  
630 freezing of social institutions and slowing down of social development: It is possible to change almost  
631 everything immediately after the establishment of a society, or a revolution that broke down current  
632 organization. However, self-maintaining institutions and forces, whose changes gradually slow down  
633 and eventually stop, accumulate in time by means of SBS. Numerous authors have highlighted this

634 aspect of cultural evolution. For example, Kováč (2015, p. 26), stressed the evolution of laws, morals,  
635 culture and political arrangements towards greater stability. Charles Sanders Pierce named this aspect  
636 of cultural evolution “the origin of habit” and “sedimentation” (see e.g. Eco, 2000). Rappaport  
637 interprets evolution as constant struggle to maintain stability that is manifested in cultural evolution by  
638 the origin, formalisation and petrification of rituals under whose paradigm the society develops  
639 (Rappaport, 1999, pp. 416, 425-437). According to Rappaport, the “aim” of all entities is to persist in  
640 the existential game as long as possible. This existential game follows the rules of evolutionarily stable  
641 strategies, whereas entities that are most stable in the context of their environment and other  
642 interacting entities persist for the longest time (Slobodkin and Rapoport, 1974; Rappaport, 1999, pp. 6-  
643 7, 408-410, 420, 422-424). However, in a similar way to biological evolution, cultural evolution also  
644 need not unidirectionally lead to absolute stability.

645 Cultural evolution usually has a punctuated character: the alternation of short periods of  
646 dynamic changes with long periods of stasis. Systems theory calls this pattern an alternation of  
647 “ultrastability” and “breaks” that occur after the deviation of an ultrastable system beyond the limits of  
648 its adaptability, which leads to its rearrangement, whether the systems are biological, economical or  
649 technological (Bardeen and Cerpa, 2015). This aspect of cultural evolution was highlighted from  
650 another angle by Lotman (2009, pp. 7-18, 114-132), who distinguished the periods of cultural “stasis”  
651 and “explosion”. Bardeen and Cerpa (2015) presented many particular examples from cultural, or  
652 technological, evolution. Numerous particular examples of the punctuated character of cultural  
653 evolution were also presented by Gould (2002, pp. 952-972). Markoš (2014) explicitly pointed out the  
654 analogy of this pattern of cultural evolution and biological punctationalism, particularly the processes  
655 described by the Frozen Plasticity Theory. In another article (Markoš, 2015), this author connects the  
656 ideas of Pierce, Lotman, Rappaport and Flegr and interprets them as various views of the general  
657 property of all semiotic systems (historical systems with evolution, ancestor–descendant relationships,  
658 memory and experiences): Original chaos “charged” with possibilities follows one specific trajectory,  
659 which is plastically changeable at the beginning, but gradually freezes and passes into the state of  
660 stasis characteristic of reversible “elastic” reactions to internal and external influences. According to

661 Markoš (2015), the evolution of all semiotic systems ends either by their expiration, or return to the  
662 original state of chaos. The biosemiotician Ostdiek (2011) analogically connects the “solidification” of  
663 the meaning of a particular symbol and the transition of a system to a state of evolutionary stasis  
664 characteristic of elastic reactions. This author even explicitly emphasizes the Frozen Plasticity Theory  
665 and argues for the homology of processes causing microevolutionary freezing and solidification of a  
666 symbol (particularly its usage by a bigger population and in a higher number of connotations and  
667 interactions with other signs and symbols) or the restoration of its original plasticity (only if the  
668 symbol loses most of its original meaning). SBS thus takes place even in cultural evolution, although,  
669 because of its specifics, SBS sometimes proceeds there in a slightly different manner than in biological  
670 evolution.

### 671 3.2 Historical dimension

672 The relatively late discovery of the principle of natural selection is considered one of the  
673 greatest enigmas of science. This principle is simple and evident from the modern point of view, yet it  
674 was not discovered until the latter half of 19<sup>th</sup> century, i.e., later than the vast majority of comparably  
675 complex and many even more complex processes in other fields (Komárek, 2003, pp. 37-44). One  
676 reason for this lateness may be cognitive bias. The human brain is specialized in solving problems of  
677 interpersonal relations, and every problem that is not easily translated into such a relation or does not  
678 have evident analogies with these relations is disproportionately harder to solve (Cosmides, 1989;  
679 Gigerenzer and Hug, 1992). For example, it was demonstrated that only a small fraction of unaware  
680 respondents solves the *Wason selection task* (Wason, 1966, 1968) easily and correctly: “You are  
681 shown 4 cards labelled A, D, 3 and 8 on the visible faces. You know that each card has a letter on one  
682 side, and a number on the other. Which card(s) must be turned over to test whether following  
683 statement applies to these 4 cards: *If a card shows A letter, then there is an odd number on the other*  
684 *side?”* On the other hand, if we translate the same task into the question on interpersonal relationships:  
685 “There are 4 persons in the bar: one elderly and one young, in which we can’t recognize the nature of  
686 their drinks, and two persons of uncertain age, one of which drinks an alcoholic beverage and the

687 second soda. Which of these persons must be controlled by a policeman to test whether the bar serves  
688 alcohol to minors?”, it is solved easily and correctly by nearly everyone.

689         The concept of *sociomorphic modelling* (Komárek, 2009) shows that Darwin’s model of  
690 natural selection, which explains the evolution of organisms as the consequence of competition of  
691 individuals for the highest fitness, could not have been generally thought of and formulated until 19<sup>th</sup>  
692 century England, in which analogous competition among individual economical subjects led to  
693 striking and immensely fast development in industry and society. The process of industrial  
694 development based on the prosperity of successful and demise of unsuccessful companies was easily  
695 thought of, which greatly facilitated insight into an analogical process among living organisms. It is no  
696 coincidence that a more or less identical model of evolution was independently formulated by  
697 Matthew (1831), Darwin (1859; Darwin and Wallace, 1858) and Wallace (Darwin and Wallace, 1858)  
698 within a few years. It is true that ideas preceding the exact formulation of the theory of natural  
699 selection could be traced several decades back (see e.g. Rádl, 2015). However, a similar insight would  
700 be much more difficult just 100–200 years earlier—back then, there was almost no substantial  
701 industrial development and companies; rather, craftsmen workshops were associated with guilds that  
702 guaranteed stable prices and quality of their products, and offered practically the same spectrum of  
703 products as they did for centuries (Ogilvie, 2004).

704         On the other hand, the very same rapid development of the material world that has surrounded  
705 us until now might have precluded the identification of another universal process that drives biological  
706 evolution—SBS—until recently. It is telling that this process was known already in ancient Greece  
707 and some historical models of biological evolution were based exclusively on it. For example,  
708 Empedocles formulated a model of the origin of living organisms through random combinations of  
709 individual limbs (i.e., organs) (Campbell, 2000). Most organisms that arose this way were not  
710 successful or even viable because their randomly combined limbs did not fit together very well.  
711 However, some of these organisms proved to be well organized, were successful and persistent, and  
712 prevailed. Thus, we cannot exclude the possibility that we will not be able to fully recognize and  
713 appreciate the true value of the most universal process that drives the evolution of practically all living

714 and non-living systems until the rapid development of our material world slows down or ceases  
715 completely.

### 716 3.3 Conclusion

717 Natural selection is neither the only, nor the most general process that drives biological  
718 evolution. It is a manifestation of a more general but underestimated *persistence principle* (Pascal and  
719 Pross, 2014, 2015, 2016), for whose temporal—and hence evolutionary—consequences we have  
720 proposed the name “stability-based sorting”. We believe that this neutral term may enable the  
721 unification of different approaches to the study of SBS-related phenomena and facilitate the  
722 interconnection of different narrowly focused field-specific studies on this topic with related general  
723 theoretical-biological concepts.

724 Our broad concept of stability that consists of (1) static stability and SBS in its strict sense and  
725 usual conception, i.e. the accumulation of temporally persistent unchanging entities and characters,  
726 and (2) sorting based on dynamic stability, i.e. selection, being a special case of this phenomenon in  
727 systems of entities replicating with heredity (see Fig. 1) has broader scope than any other attempt to  
728 study these phenomena in the field of evolutionary biology or related disciplines. Therefore, despite  
729 our primary goal was to show the paramount importance of the effects of SBS on various levels of  
730 diverse evolutionary systems—a fact that has been practically neglected among evolutionary  
731 biologists—our conception may also serve as a new standpoint and universal platform for students of  
732 various kinds of evolving systems.

733 All complex novelties in biological evolution originate from the joint influence of two kinds  
734 of SBS in the broad sense, the force that drive the system towards dynamic stability and the force that  
735 drive the system towards static stability. The same applies to all natural and artificial systems whose  
736 entities multiply by reproduction or copying and exhibit at least some degree of inheritance—e.g.,  
737 cultural evolution or even simulated systems with those properties. Indeed, there are clear analogies  
738 between the SBS-related phenomena observed in various kinds of evolving systems, for example, the  
739 punctuated character of their evolution or increasing resistance to change (see e.g. Post and Pimm,

740 1983; Ostdiek, 2011; Markoš, 2014, 2015). Explanatory framework based on SBS thus could provide  
741 new insight into the evolution of any complex system.

742 In future, simulations that recognize the difference between *static* and *dynamic* nature of the  
743 sorting the evolving systems undergo and discriminate the role of these two kinds of sorting under  
744 various parameters may significantly contribute to the understanding of the general rules of evolution  
745 of any systems, and, consequentially, our theoretical understanding of some of the most profound  
746 phenomena of existence—e.g., the nature of life.

## 747 4 Appendix

### 748 4.1 The relationship between the presented concept and the conception of Pross et al.

749 Pross (2003, 2004, 2012), Wagner and Pross (2011) and Pascal and Pross (2014, 2015, 2016  
750 and references therein) studied the role of stability in nature thoroughly, differentiating static  
751 thermodynamic stability that affects non-living entities and dynamic kinetic stability that is based on  
752 replicative chemistry and characteristic of living entities. The identification of the exact physical basis  
753 of the stability kinds is out of scope of this article. However, the equation of static stability to  
754 thermodynamic stability, i.e. the state of highest entropy (Pross, 2003, 2004, 2012; Wagner and Pross,  
755 2011; Pascal and Pross, 2014, 2015, 2016), is an evident one. Pross and his colleagues stress that this  
756 kind of stability is fundamentally different to dynamic kinetic stability based on replicative chemistry  
757 and Malthusian kinetics, whereas the two stability kinds are unified under the umbrella of purely  
758 logical *persistence principle*: The general tendency of systems to change from less stable (persistent)  
759 to more stable (persistent) forms (Pascal and Pross, 2014, 2015, 2016).

760 Our conception that integrates all evolutionary systems regardless their physical basis is  
761 slightly different (see Fig. 1). In our concept, thermodynamic stability is just one option how to ensure  
762 static stability, although it could be speculated whether all other options (regarding e.g. immaterial  
763 entities such as memes, or even dynamically stable entities) could be ultimately converted or do  
764 naturally converge onto this one. Dynamic stability in our conception is not defined by the physical  
765 properties of particular system (i.e. replicative chemistry) either. Although the degree of dynamic

766 stability must depend on the Malthusian kinetics of the dynamically stable entities (it would probably  
767 be better to say context dependent evolutionary stability in the sense of evolutionary stable strategies  
768 of Maynard Smith and Price, 1973) as in the Pross' concept, we stress especially the second, somehow  
769 "static", aspect of this sorting—heredity. Dynamic stability in our concept can be explicated as a  
770 special case of static stability in which the stable sorted "thing" changed from the entity itself to the  
771 heritable information necessary for its copying or reproduction. Therefore, static stability in our  
772 conception is more general and *de facto* corresponds to Pross' general persistence in time or  
773 *persistence principle* (see Fig. 1).

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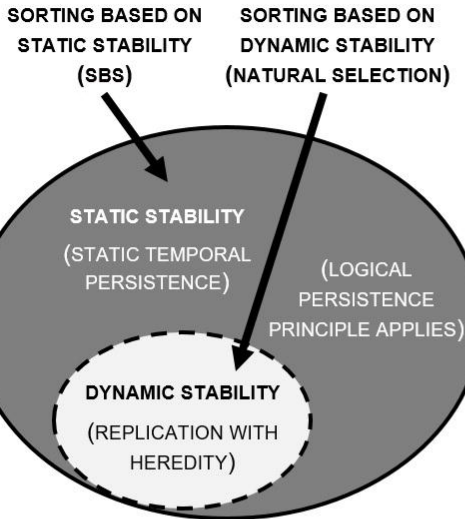
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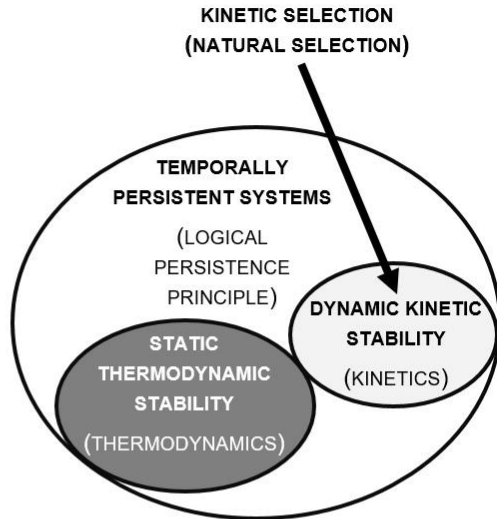


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A



B



**Fig. 1.** The difference between presented stability concept (A) and the stability concept of Pross et al. (B). We differentiate two kinds of stability (A). Static stability equates to the entity's static stability in time, i.e. its persistence until its expiration or change into something else, regardless of the physical basis of this process. Statically more stable entities and their properties are sorted in time in the process of SBS. Entities replicating with heredity are sorted, or selected, on the basis of dynamic stability, i.e. largest difference between the speed of generation and expiration of their copies. Putting aside its physical basis and viewed from the evolutionary perspective, however, dynamic stability is only a special case of static stability in systems of entities replicating with heredity in which the statically sorted "thing" became the *information* how to copy itself. Pross (2003, 2004, 2012), Wagner and Pross (2011) and Pascal and Pross (2014, 2015, 2016), on the other hand (B), differentiate static thermodynamic stability and dynamic kinetic stability. Both of these stability kinds, i.e. the state of high entropy and the exponential multiplication of entities, are governed by the general logical "persistence principle": systems' tendency to change from less stable (persistent) to more stable (persistent). Note that other kinds of stable systems may eventually exist and be subject to the *persistence principle*. Dynamic kinetic stability equates dynamic stability in the first concept; kinetic selection indeed was proposed to be equal to natural selection (Pross, 2004, 2012). It is its relationship to static stability that differs among the two concepts. Note, (1) that our approach is more general, addresses all material and immaterial entities, and does not address the physical basis of stability, and therefore (2) the difference is mainly conceptual—both approaches need not exclude each other.