1 # Stability-based sorting: The forgotten

2 # process behind (not only) biological

3 # evolution

4 Authors (given name first)

5 Jaroslav Flegr[1]*

6 Jan Toman[1]

7 1: Laboratory of Evolutionary Biology, Department of Philosophy and History of Sciences, Faculty of

8 Science, Charles University in Prague, Vinicna 7, 128 00 Prague 2, Czech Republic

9 J. Toman: tomanj@natur.cuni.cz

10 J. Flegr: flegr@cesnet.cz, tel.: +(420)221951821

11 * Corresponding author

12

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 long-term 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 evolution—especially 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.

Keywords

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, 1860). 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 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 meta-adaptations (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

62   Selfish Gene (Dawkins, 1976, p. 13[1]). 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*

---

[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."

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.

2   Results and Discussion

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[2]. 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

---

[2]   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)[3]. 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.

---

[3]   "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)[4]. Only e*x 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

---

[4]   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

13

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[5]. 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,

---

[5]   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 Eldgredge and

411   Gould (1972)[6]. 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

---

[6]   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 paleotaxonomists 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

20

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 (Glenner 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)[7]. 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).

---

[7] 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

24

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 punctuationalism, 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 19th 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 19th

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.

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.

4   Appendix

747

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

748

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).

5   Acknowledgment

774

6   References

780

781   Alroy, J., 2008. Dynamics of origination and extinction in the marine fossil record. Proceedings of the

782   National Academy of Sciences of the United States of America 105, 11536-11542,

783   doi:10.1073/pnas.0802597105.

784   Bardeen, M., 2009. Lessons from Daisyworld. Survival of the stable., Centre for Computational

785   Neuroscience and Robotics, Vol. Ph. D. University of Sussex, Brighton, UK, pp. 93.

786   Bardeen, M., Cerpa, N., 2015. Editorial: Technological Evolution in Society - The Evolution of

787   Mobile Devices. Journal of Theoretical and Applied Electronic Commerce Research 10, 1-7.

788   Bartolomei, M., Tilghman, S., 1997. Genomic imprinting in mammals. Annual Review of Genetics 31,

789   493-525.

790   Becerra, M., Brichette, I., Garcia, C., 1999. Short-term evolution of competition between genetically

791   homogeneous and heterogeneous populations of *Drosophila melanogaster*. Evolutionary

792   Ecology Research 1, 567-579.

793   Benton, M., 1995. diversification and extinction in the history of life. Science 268, 52-58,

794   doi:10.1126/science.7701342.

795   Bernstein, H., Bernstein, C., 2013. Evolutionary origin and adaptive function of meiosis. In: Bernstein,

796   H., Bernstein, C., Eds.), Meiosis, Vol. 1. InTech, Available from:

797   http://www.intechopen.com/books/meiosis/evolutionary-origin-and-adaptive-function-of-

798   meiosis.

799   Birdsell, J., Wills, C., 2003. The evolutionary origin and maintenance of sexual recombination: A

800   review of contemporary models. Evolutionary Biology, Vol 33 33, 27-138.

801   Blackmore, S., 1999. The Meme Machine. Oxford University Press, New York.

802   Bouchard, F., 2008. Causal Processes, Fitness, and the Differential Persistence of Lineages.

803   Philosophy of Science 75, 560-570.

804   Bouchard, F., 2011. Darwinism without populations: a more inclusive understanding of the "Survival

805   of the Fittest". Studies in History and Philosophy of Science Part C: Studies in History and

806   Philosophy of Biological and Biomedical Sciences 42, 106-114.

807   Bourrat, P., 2014. From survivors to replicators: evolution by natural selection revisited. Biology &

808   Philosophy 29, 517-538, doi:10.1007/s10539-013-9383-1.

809   Brusatte, S., Lloyd, G., Wang, S., Norell, M., 2014. Gradual Assembly of Avian Body Plan

810   Culminated in Rapid Rates of Evolution across the Dinosaur-Bird Transition. Current Biology

811   24, 2386-2392, doi:10.1016/j.cub.2014.08.034.

812   Campbell, G., 2000. Zoogony and Evolution in Plato's Timaeus: The Prescoratics, Lucretius and

813   Darwin. In: Wright, M., (Ed.), Reason and Necessity: Essays on Plato's Timaeus. Duckworth

814   and the Classical Press of Wales, London, pp. 145-180.

815   Canning, E., Okamura, B., Baker, J., Muller, R., Rollinson, D., 2004. Biodiversity and evolution of the

816   myxozoa. Advances in Parasitology, Vol 56 56, 43-131, doi:10.1016/S0065-308X(03)56002-

817   X.

818   Chiappe, L., 2009. Downsized Dinosaurs: The Evolutionary Transition to Modern Birds. Evolution:

819   Education and Outreach 2, 248-256.

820   Cosmides, L., 1989. The logic of social exchange: Has natural selection shaped how humans reason?

821   Studies with the Wason selection task. Cognition 31, 187-276.

822   Darwin, C., 1859. On the origin of species by means of natural selection or the preservation of

823   favoured races in the struggle for life. John Murray, London.

824   Darwin, C., Wallace, A., 1858. On the Tendency of Species to form Varieties; and on the Perpetuation

825   of Varieties and Species by Natural Means of Selection. Journal of the proceedings of the

826   Linnean Society of London. Zoology. 3, 45-62.

827   Davison, J., 1998. Evolution as a self-limiting process. Rivista Di Biologia-Biology Forum 91, 199-

828   220.

829   Dawkins, R., 1976. Selfish gene. Oxford University Press, Oxford.

830   Dawkins, R., 1982. The Extended Phenotype: The Long Reach of the Gene. Oxford University Press,

831   Oxford, UK; New York, USA.

832   Dececchi, T., Larsson, H., 2013. Body and limb size dissociation at the origin of birds: uncoupling

833   allometric constraints across a macroevolutionary transition. Evolution 67, 2741-2752,

834   doi:10.1111/evo.12150.

835   DiMichele, W., Bateman, R., 1996. Plant paleoecology and evolutionary inference: Two examples

836   from the Paleozoic. Review of Palaeobotany and Palynology 90, 223-247, doi:10.1016/0034-

837   6667(95)00085-2.

838   Dobzhansky, T., 1964. How do the genetic loads affect the fitness of their carriers in *Drosophila*

839   populations? American Naturalist 98, 151-166.

840   Doolittle, W., 1981. Is nature really motherly? CoEvolution Quarterly 29, 59-63.

841   Doolittle, W., 2014. Natural selection through survival alone, and the possibility of Gaia. Biology &

842   Philosophy 29, 415-423, doi:10.1007/s10539-013-9384-0.

843   Douzery, E., Snell, E., Bapteste, E., Delsuc, F., Philippe, H., 2004. The timing of eukaryotic evolution:

844   does a relaxed molecular clock reconcile proteins and fossils? Proceedings of the National

845   Academy of Sciences of the United States of America 101, 15386-15391,

846   doi:10.1073/pnas.0403984101.

847   Eble, G., 1998. The role of development in evolutionary radiations. In: McKinney, M., Drake, J.,

848   Eds.), Biodiversity dynamics: turnover of populations, taxa, and communities. Columbia

849   University Press, New York, pp. 132-161.

850   Eble, G., 1999. Originations: Land and sea compared. Geobios 32, 223-234, doi:10.1016/S0016-

851   6995(99)80036-9.

852   Eco, U., 2000. Kant and the Platypus: Essays on Language and Cognition. Houghton Mifflin Harcourt,

853   USA.

854   Eldredge, N., Gould, S., 1972. Punctuated equilibria: an alternative to phyletic gradualism. In: Schopf,

855   T. J. M., (Ed.), Models in Paleobiology. Freeman, Cooper and Co., San Francisco, pp. 82-115.

856   Erwin, D., 2007. Disparity: Morphological pattern and developmental context. Palaeontology 50, 57-

857   73, doi:10.1111/j.1475-4983.2006.00614.x.

858   Erwin, D., Valentine, J., Sepkoski, J., 1987. A comparative study of diversification events: the early

859   Paleozoic versus the Mesozoic. Evolution 41, 1177-1186, doi:10.2307/2409086.

860   Erwin, D., Laflamme, M., Tweedt, S., Sperling, E., Pisani, D., Peterson, K., 2011. The Cambrian

861   Conundrum: Early Divergence and Later Ecological Success in the Early History of Animals.

862   Science 334, 1091-1097, doi:10.1126/science.1206375.

863   Fernald, R., 2000. Evolution of eyes. Current Opinion in Neurobiology 10, 444-450,

864   doi:10.1016/S0959-4388(00)00114-8.

865   Flegr, J., 1997. Two distinct types of natural selection in turbidostat-like and chemostat-like

866   ecosystems. Journal of Theoretical Biology 188, 121-126, doi:10.1006/jtbi.1997.0458.

867   Flegr, J., 1998. On the "origin" of natural selection by means of speciation. Rivista Di Biologia-

868   Biology Forum 91, 291-304.

869   Flegr, J., 2008. Frozen evolution: Or, that's not the way it is, mr. Darwin - Farewell to selfish gene.

870   Createspace Independent Pub., USA.

871   Flegr, J., 2010. Elastic, not plastic species: frozen plasticity theory and the origin of adaptive evolution

872   in sexually reproducing organisms. Biology Direct 5, -, doi:ARTN 2 DOI 10.1186/1745-6150-

873   5-2.

874   Flegr, J., 2013. Microevolutionary, macroevolutionary, ecological and taxonomical implications of

875   punctuational theories of adaptive evolution. Biology Direct 8, doi:10.1186/1745-6150-8-1.

876   Foote, M., 1997. The evolution of morphological diversity. Annual Review of Ecology and

877   Systematics 28, 129-152, doi:10.1146/annurev.ecolsys.28.1.129.

878   Gigerenzer, G., Hug, K., 1992. Domain-specific reasoning: Social contracts, cheating, and perspective

879   change. Cognition 43, 127-171, doi:10.1016/0010-0277(92)90060-U.

880   Gilinsky, N., 1994. Volatility and the Phanerozoic decline of background extinction intensity.

881   Paleobiology 20, 445-458.

882   Gilinsky, N., Bambach, R., 1987. Asymmetrical patterns of origination and extinction in higher taxa.

883   Paleobiology 13, 427-445.

884   Glenner, H., Hebsgaard, M., 2006. Phylogeny and evolution of life history strategies of the Parasitic

885   Barnacles (Crustacea, Cirripedia, Rhizocephala). Molecular Phylogenetics and Evolution 41,

886   528-538, doi:10.1016/j.ympev.2006.06.004.

887   Godfrey-Smith, B., 2009. Darwinian populations and natural selection. Oxford University Press, USA.

888   Gorelick, R., Heng, H., 2011. Sex reduces genetic variation: a multidisciplinary review. Evolution 65,

889   1088-1098, doi:10.1111/j.1558-5646.2010.01173.x.

890   Gould, S., 1988. Kropotkin was no crackpot. Natural History 97, 12-21.

891   Gould, S., 1989. Wonderful Life: The Burgess Shale and the Nature of History. W. W. Norton &

892   Company, New York, London.

893   Gould, S., 2002. The Structure Of Evolutionary Theory. The Belknap Press of Harvard University

894   Press, Cambridge Massachusetts, London England

895   Grand, S., 2001. Creation: Life and how to make it. Harvard University Press, Cambridge, USA.

896   Hughes, M., Gerber, S., Wills, M., 2013. Clades reach highest morphological disparity early in their

897   evolution. Proceedings of the National Academy of Sciences of the United States of America

898   110, 13875-13879, doi:10.1073/pnas.1302642110.

899 Hörandl, E., 2013. Meiosis and the paradox of sex in nature. In: Bernstein, H., Bernstein, C., Eds.),

900   Meiosis, Vol. 1. InTech, Available from:

901   http://www.intechopen.com/books/meiosis/evolutionary-origin-and-adaptive-function-of-

902   meiosis.

903 Jablonski, D., 2002. Survival without recovery after mass extinctions. Proceedings of the National

904   Academy of Sciences of the United States of America 99, 8139-8144,

905   doi:10.1073/pnas.102163299.

906 Kolokoltsov, V., Malafeyev, O., 2010. Understanding Game Theory: Introduction to the Analysis of

907   Many Agent Systems with Competition and Cooperation. World Scientific Publishing Co. Pte.

908   Ltd., New Jersey, London, Singapore, Beijing, Shanghai, Hong Kong, Taipei, Chennai.

909 Komárek, S., 2003. Mimicry, aposematism and related phenomena: Mimetism in nature and the

910   history of its study. LINCOM EUROPA, Muenchen.

911 Komárek, S., 2009. Nature and culture: The world of phenomena and the world of interpretation.

912   LINCOM Europa, München.

913 Kováč, L., 2015. Closing Human Evolution: Life in the Ultimate Age. Springer, Cham, Heidelberg,

914   New York, Dordrecht, London.

915 Laland, K., Uller, T., Fellman, M., Sterelny, K., Muller, G., Moczek, A., Jablonka, E., Odling-Smee,

916   J., 2015. The extended evolutionary synthesis: its structure, assumptions and predictions.

917   Proceedings of the Royal Society B-Biological Sciences 282, doi:10.1098/rspb.2015.1019.

918 Lehtonen, J., Jennions, M., Kokko, H., 2012. The many costs of sex. Trends in Ecology & Evolution

919   27, 172-178, doi:10.1016/j.tree.2011.09.016.

920 Leigh, E., 2010. The group selection controversy. Journal of Evolutionary Biology 23, 6-19,

921   doi:10.1111/j.1420-9101.2009.01876.x.

922 Lloyd, G., Wang, S., Brusatte, S., 2012. Identifying heterogeneity in rates of morphological evolution:

923   discrete character change in the evolution of lungfish (Sarcopterygii; Dipnoi). Evolution 66,

924   330-348, doi:10.1111/j.1558-5646.2011.01460.x.

925 Lotka, A., 1922a. Contribution to the energetics of evolution. Proceedings of the National Academy of

926   Sciences of the United States of America 8, 147–151, doi:-.

927   Lotka, A., 1922b. Natural selection as a physical principle. Proceedings of the National Academy of

928   Sciences of the United States of America 8, 151–154, doi:-.

929   Lotman, J., 2009. Culture and Explosion. Walter de Gruyter GmbH & Co., Berlin.

930   Lovelock, J., 1979. Gaia: A New Look at Life on Earth. Oxford University Press, Oxford, UK.

931   Markoš, A., 1995. The ontogeny of Gaia: the role of microorganisms in planetary information

932   network. Journal of Theoretical Biology 176, 175-180, doi:10.1006/jtbi.1995.0186.

933   Markoš, A., 2002. Readers of the Book of Life: Contextualizing Developmental Evolutionary Biology.

934   Oxford University Press.

935   Markoš, A., 2014. Biosphere as semiosphere: Variations on Lotman. Sign System Studies 42, 487-

936   498.

937   Markoš, A., 2015. The Birth and Life of Species–Cultures. Biosemiotics, 1-12.

938   Matthew, P., 1831. On naval timber and arboriculture: with critical notes on authors who have recently

939   treated the subject of planting. Adam Black; Longman, Rees, Orme, Brown, and Green,

940   Edinburgh, London.

941   Maynard Smith, J., Price, G., 1973. The logic of animal conflict. Nature 263, 15-18.

942   Maynard Smith, J., Szathmáry, E., 2010. The major transitions in evolution. Oxford University Press

943   Inc., New York.

944   Mayr, E., 2003. The Growth of Biological Thought: Diversity, Evolution, and Inheritance. The

945   Belknap Press of Harvard University Press, Cambridge, Massacusetts; London, UK.

946   McInerney, J., Pisani, D., Bapteste, E., O'Connell, M., 2011. The public goods hypothesis for the

947   evolution of life on Earth. Biology Direct 6, doi:10.1186/1745-6150-6-41.

948   Michod, R., 2000. Darwinian Dynamics: Evolutionary Transitions in Fitness and Individuality.

949   Princeton University Press, Princeton New Jersey, Chichester West Sussex.

950   Mills, D., Peterson, R., Spiegelman, S., 1967. An extracellular Darwinian experiment with a self-

951   duplicating nucleic acid molecule. Proceedings of the National Academy of Sciences 58, 217-

952   224.

953   Murchison, E., 2008. Clonally transmissible cancers in dogs and Tasmanian devils. Oncogene 27, 19-

954   30.

955   Neale, D., Marshall, K., Sederoff, R., 1989. Chloroplast and mitochondrial DNA are paternally
956   inherited in S*equoia sempervirens* D. Don Endl. Proceedings of the National Academy of
957   Sciences of the United States of America 86, 9347-9349.

958   Ogilvie, S., 2004. Guilds, efficiency, and social capital: evidence from German proto-industry. The
959   Economic History Review 57, 286-333.

960   Okasha, S., 2006. Evolution and the levels of selection. Oxford University Press, USA.

961   Ostdiek, G., 2011. Cast in Plastic: Semiotic Plasticity and the Pragmatic Reading of Darwin.
962   Biosemiotics 4, 69-82, doi:10.1007/s12304-010-9108-7.

963   Pascal, R., Pross, A., 2014. The nature and mathematical basis for material stability in the chemical
964   and biological worlds. Journal of Systems Chemistry 5, -, doi:10.1186/1759-2208-5-3.

965   Pascal, R., Pross, A., 2015. Stability and its manifestation in the chemical and biological worlds.
966   Chemical Communications 51, 16160-16165, doi:10.1039/c5cc06260h.

967   Pascal, R., Pross, A., 2016. The logic of life. Origins of Life and Evolution of Biospheres 46, 507-513,
968   doi:10.1007/s11084-016-9494-1.

969   Peterson, K., Cotton, J., Gehling, J., Pisani, D., 2008. The Ediacaran emergence of bilaterians:
970   congruence between the genetic and the geological fossil records. Philosophical Transactions
971   of the Royal Society B-Biological Sciences 363, 1435-1443, doi:10.1098/rstb.2007.2233.

972   Post, W., Pimm, S., 1983. Community assembly and food web stability. Mathematical Biosciences 64,
973   169-192, doi:10.1016/0025-5564(83)90002-0.

974   Pross, A., 2003. The driving force for life's emergence: kinetic and thermodynamic considerations.
975   Journal of theoretical biology 220, 396-406.

976   Pross, A., 2004. Extending the concept of kinetic stability: toward a paradigm for life. Journal of
977   physical organic chemistry 17, 312-316.

978   Pross, A., 2012. What is life? How chemistry becomes biology. Oxford University Press, Oxford, UK.

979   Rappaport, R., 1999. Ritual and Religion in the Making of Humanity. Cambridge University Press,
980   New York, USA, pp. 535.

981   Rasnicyn, A., 2005. Collected works in evolutionary biology (Izbrannye trudy po evolucionnoj
982   biologii). Tovarisevstvo naucnych izdanii KMK, Moscow.

983   Raup, D., Sepkoski, J., 1982. Mass extinctions in the marine fossil record. Science 215, 1501-1503,

984   doi:10.1126/science.215.4539.1501.

985   Ray, T., 1993. An Evolutionary Approach to Synthetic Biology: Zen and the Art of Creating Life.

986   Artificial Life 1, 179-209.

987   Ray, T., 1997. Evolving complexity. Artificial Life and Robotics 1, 21-26.

988   Ray, T., Hart, J., 1998. Evolution of differentiated multi-threaded digital organisms. In: Adami, C., et

989   al., Eds.), Artificial Life VI: Proceedings of the Sixth International Conference on Artificial

990   Life. MIT Press, Canbridge Massachusetts, London England, pp. 295-306.

991   Redfield, R., 2001. Do bacteria have sex? Nature Reviews Genetics 2, 634-639.

992   Rohde, R., Muller, R., 2005. Cycles in fossil diversity. Nature 434, 208-210, doi:10.1038/nature03339.

993   Rosa, D., 1899. La Riduzione progressiva della variabilità e i suoi rapporti coll'estinzione e

994   coll'origine delle specie. Clausen, Torino.

995   Runarsson, T., Jonsson, M., 1999. Genetic production systems for intelligent problem solving. Journal

996   of Intelligent Manufacturing 10, 181-186, doi:10.1023/A:1008928804949.

997   Rádl, E., 2015. The history of biological theories. BiblioLife, USA.

998   Safuta, J., 2011. Spacetime deformations evolution concept. arXiv.

999   Shcherbakov, V., 2010. Biological species is the only possible form of existence for higher organisms:

1000   the evolutionary meaning of sexual reproduction. Biology Direct 5, doi:10.1186/1745-6150-5-

1001   14.

1002   Shcherbakov, V., 2012. Stasis is an Inevitable Consequence of Every Successful Evolution.

1003   Biosemiotics 5, 227-245, doi:10.1007/s12304-011-9122-4.

1004   Shcherbakov, V., 2013. Biological Species as a Form of Existence, the Higher Form. In: Pavlinov, I.,

1005   (Ed.), The Species Problem - Ongoing Issues. InTech, Rijeka, Croatia, pp. 65-91.

1006   Sheldon, P., 1996. Plus ça change–a model for stasis and evolution in different environments.

1007   Palaeogeography Palaeoclimatology Palaeoecology 127, 209-227.

1008   Shu, D., 2008. Cambrian explosion: Birth of tree of animals. Gondwana Research 14, 219-240,

1009   doi:10.1016/j.gr.2007.08.004.

Simon, H., 1962. The architecture of complexity. Proceedings of the American Philosophical Society 106, 467-482.

Slobodkin, L., Rapoport, A., 1974. An Optimal Strategy of Evolution. The Quarterly Review of Biology 49, 181-200.

Slotine, J., 1994. Stability in adaptation and learning. In: Cliff, D., (Ed.), From animals to animats 3. MIT Press, Brighton, England, pp. 30-34.

Slotine, J., 2003. Modular stability tools for distributed computation and control. International Journal of Adaptive Control and Signal Processing 17, 397-416, doi:10.1002/acs.754.

Slotine, J., Lohmiller, W., 2001. Modularity, evolution, and the binding problem: a view from stability theory. Neural Networks 14, 137-145, doi:10.1016/S0893-6080(00)00089-7.

Stanley, S., 1979. Macroevolution, Pattern and Process. W.H. Freeman and Company, San Francisco.

Syvanen, M., 2002. Recent emergence of the modern genetic code: a proposal. Trends in Genetics 18, 245-248, doi:10.1016/S0168-9525(02)02647-1.

Thearling, K., Ray, T., 1994. Evolving Multi-cellular Artificial Life. In: Brooks, R., Maes, P., Eds.), Artificial Life IV: Proceedings of the Fourth International Workshop on the Synthesis and Simulation of Living Systems. MIT Press, Cambridge Massachusetts, London England, pp. 283-288.

Thearling, K., Ray, T., 1996. Evolving parallel computation. Complex Systems 10, 229-237.

Van Valen, L., 1973. A new evolutionary law. Evolutionary Theory 1, 1-30.

Van Valen, L., 1989. Three paradigms of evolution. Evolutionary Theory 9, 1-17.

Vrba, E., Gould, S., 1986. The hierarchical expansion of sorting and selection: sorting and selection cannot be equated. Paleobiology 12, 217-228.

Wagner, N., Pross, A., 2011. The nature of stability in replicating systems. Entropy 13, 518-527.

Walker, L., del Moral, R., 2003. Primary Succession and Ecosystem Rehabilitation. Cambridge University Press, Cambridge, UK.

Ward, P., 2009. The Medea Hypothesis: Is Life on Earth Ultimately Self-Destructive? Princeton University Press, Princeton, USA; Oxford, UK.

1037   Wason, P., 1966. Reasoning. In: Foss, B., (Ed.), New Horizons in Psychology, Vol. 1. Penguin Books,

1038   Harmondsworth, UK, pp. 135-151.

1039   Wason, P., 1968. Reasoning about a rule. Quarterly Journal of Experimental Psychology 20, 273-281,

1040   doi:10.1080/14640746808400161.

1041   Weber, B., Depew, D., 1996. Natural Selection and Self-Organization: Dynamical Models as Clues to

1042   a New Evolutionary Synthesis. Biology and Philosophy 11, 33-65.

1043   Webster, M., 2007. A Cambrian peak in morphological variation within trilobite species. Science 317,

1044   499-502, doi:10.1126/science.1142964.

1045   Williams, G. C., 1975. Sex and evolution. Princeton University Press, Princeton, NJ.

1046   Wilson, D., 1983. The group selection controversy: history and current status. Annual Review of

1047   Ecology and Systematics 14, 159-187, doi:10.1146/annurev.es.14.110183.001111.

1048   Wimsatt, W., 1980. The units of selection and the structure of the multi-level genome. In: Asquithand,

1049   P., Giere, R., Eds.), PSA: Proceedings of the Biennial Meeting of the Philosophy of Science

1050   Association, Vol. 2. Philosophy of Science Association, East Lansing, MI, pp. 122-183.

1051   Wright, S., 1932. The roles of mutation, inbreeding, crossbreeding, and selection in evolution. In:

1052   Jones, D., (Ed.), Proceedings of the Sixth International Congress on Genetics. Brooklyn

1053   botanic garden, New York, pp. 356-366.

1054   Wynne-Edwards, V., 1986. Evolution Through Group Selection. Blackwell Scientific Publications,
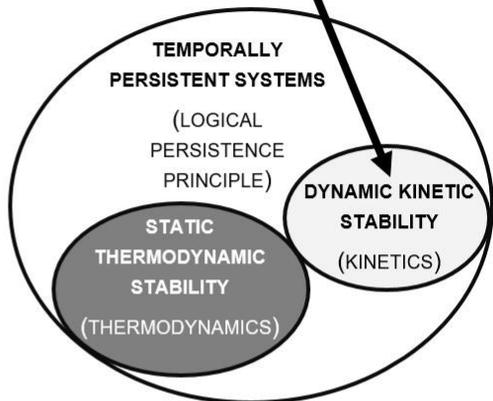
1055   Oxford.
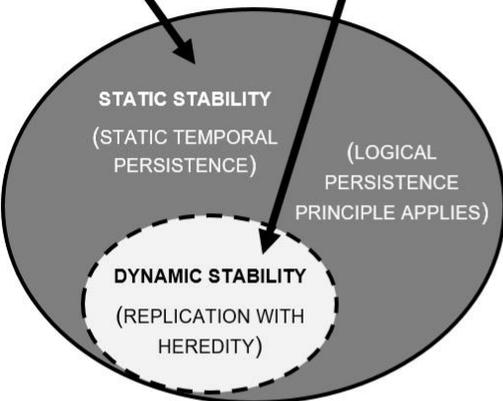
Fig. 1. The difference between presented stability concept (A) and the stability concept of Pross et al. (B). We differentiate two kinds of stability (A). Static stability equates to the entity's static stability in time, i.e. its persistence until its expiration or change into something else, regardless 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.