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2 **On the advantages of low evolvability in fluctuating environments: could sex be the**
3 **preadaptation for the stability-based sorting?**

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5 Running title: Advantages of low evolvability

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22 plasticity; punctuated equilibrium.

23

24 **Abstract**

25 The ability of organisms to adaptively respond to environmental changes (evolvability) is usually
26 considered to be an important advantage in interspecies competition. It has been suggested, however,
27 that evolvability could be a double-edged sword that could turn into a serious handicap in fluctuating
28 environments. The authors of this counterintuitive idea have published only verbal models to support
29 their claims.

30 Here we present the results of individual-based stochastic modelling of competition between two
31 asexual species differing only by their evolvability. They show that, in changeable environments, less
32 evolvable species could outperform its more evolvable competitor in a broad area of a parameter
33 space, regardless of whether the conditions fluctuated periodically or aperiodically. Highly evolvable
34 species prospered better nearly all the time; however, they sustained a higher probability of extinction
35 during rare events of rapid transient change of conditions.

36 Our results offer an explanation of why sexually reproducing species, with their reduced capacity to
37 respond adaptively to environmental changes, prevail in most eukaryotic taxa in nearly all biotopes on
38 the surface of Earth. These species often suffer several important disadvantages in direct competition
39 with asexual species; however, they mostly win in changeable environments in the more important
40 sorting-according-to-stability battle.

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43 **Introduction**

44 Most of the eukaryotic organisms on Earth reproduce sexually, despite the existence of many obvious
45 disadvantages, including two twofold costs of this complicated mode of reproduction (the cost of
46 meiosis and the cost of males), of this complicated mode of reproduction (Otto, 2009). Many models
47 and hypotheses have been published within the past 40 years to describe the conditions under which
48 sexually reproducing organisms can outperform their asexual competitors, including asexual mutants
49 (Bell, 1982; Maynard Smith, 1978). For most of these models (except, e.g., for the DNA repairing
50 models (Horandl & Hadacek, 2013) or variants of Muller ratchet models (Kondrashov, 1982; Muller,
51 1964)), such conditions are relatively special and occur only in certain ecological situations. At the
52 same time, sexual reproduction is predominant in all groups of eukaryotic organisms regardless of
53 their taxonomic position or ecological strategy (Charlesworth, 2006). Moreover, the obligate sex
54 prevails in many taxa, despite the fact that it is nearly always outperformed by the facultative sex, the
55 condition-dependent alternation of many rounds of asexual reproduction with a round or rounds of
56 sexual reproduction (Bell, 1982; Green & Noakes, 1995).

57 An interesting verbal model explaining the origin and persistence of sexual reproduction was
58 suggested by Williams (1975), in his seminal book *Sex and Evolution* pp. 145-146, 149-154, 169. He
59 argued that, paradoxically, sexual species can take advantage of their lower ability to evolve. Due to
60 the negative influence of segregation and recombination on the heritability of phenotypic traits and
61 fitness, and due to the effect of gene flow, the ability of populations of sexual species to adapt to
62 actual environmental conditions is lower in comparison with populations of asexual species.
63 Therefore, populations of sexual species usually retain a large part of their genetic polymorphism,
64 including alleles that are suboptimal under present local conditions. Such alleles usually persist in the
65 population at low frequencies, but their presence can be extremely useful for the survival of the
66 population and species when local conditions change.

67 It was also suggested recently that one of the important differences between asexual and
68 sexual organisms is a much higher incidence of frequency-dependent selection (Flegr, 2010). Together
69 with pleiotropy and epistasis, the presence of certain amount (possibly not too high amount) of alleles
70 with such frequency dependent effects on fitness could stabilize the composition of the gene pool of a
71 population, which would strongly decrease its ability responding to directional selection. One of the
72 implications of this theory is that sexual species are favored in randomly or periodically fluctuating
73 environments, i.e., in most environments on the surface of Earth, due to their lower evolvability. The
74 stabilization of the composition of the gene pool not only prevents the population from the elimination
75 of momentarily suboptimal alleles (Williams, 1975) but also decreases its ability to respond to
76 selection, and by doing so, protects the population against an adaptation to transient changes in its
77 environment (Flegr, 2013).

78 The counterintuitive idea of Williams, which can be in fact traced back to Darwin (Darwin,
79 Barrett, & Freeman, 1987), has been theoretically studied by several authors in the context of the
80 origin and maintenance of amphimixis, for review see (Kondrashov, 1993). The models show that
81 under special conditions (special genetic architecture, alternating pure stabilizing and disruptive
82 selection, etc.), the sexually reproducing organisms can outperform their asexual competitors (Gandon
83 & Otto, 2007; Roughgarden, 1991). However, the character of environmental fluctuation favoring low
84 evolvability has never been studied in detail. The aim of the present study is to test the validity of the
85 verbal models of Williams (1975) and Flegr (2013) using a numeric individual-based stochastic
86 model. Specifically, we searched for combinations of parameters under which the inability to
87 adaptively respond to selection alone (not in the combination with amphimixis) is advantageous and
88 may result in the victory of less evolvable species over its more evolvable competitor. In contrast to
89 others, we studied the behavior of a model of competition between two asexual species: the more
90 evolvable asexual species, which can freely respond to selection (plastic species), and the less
91 evolvable asexual species, whose members are penalized for deflecting from its original phenotype
92 (elastic species). This allows us to distinguish whether the species overran its competitor due to its
93 evolutionary passivity alone or due to other advantages of sexuality, such as its higher genetic
94 polymorphism – the existence of a stock of potentially useful alleles.

95

96 **Methods**

97 *Model*

98 The time in our stochastic, individual-based model is discrete, i.e., all births and deaths and
99 environmental changes happen simultaneously, and is measured in generations. In each generation
100 individuals propagate with a given probability and died with another probability. Therefore, each
101 generation can be considered as one reproduction period of a species. We used this model for studying
102 the competition of two species, plastic and elastic asexual species, living in an unstructured
103 environment characterized by one (periodically or aperiodically fluctuating) environmental variable
104 E_{env} , e.g., temperature. In the periodically fluctuating environment, the current temperature, and at the
105 same time the optimal temperature for an organism to be adapted to, E_{env} , is represented by a sinusoid
106 that is characterized by its amplitude A and period T . Fig. 1a shows the E_{env} curve (red line) for
107 amplitude 1.3 and period 500. The aperiodic conditions are described by a stochastic curve with
108 particular amplitude A , generated by randomly adding or subtracting the constant increment ΔE
109 to/from E_{env} with probability P_E per generation. Here, the rate of the environmental change is
110 characterized by the pseudoperiod T (determined by the combination of ΔE and P_E), which is
111 numerically equal to such a period T of the periodic model, for which the average speed of E_{opt} change

112 from $-A$ to A is the same for both models. The value of ΔE was fixed to 0.2 and P_E for each
113 pseudoperiod was computed in advance by the Monte Carlo method. The value of E_{env} is bounded –
114 when after an increment, it would exceed A (or fall below $-A$), it is reset to A (or $-A$). Fig. 2a shows a
115 stochastic curve E_{env} (red line) with amplitude 1.2, $\Delta E = 0.2$, and $P_E = 0.2$. For both periodical and
116 aperiodical conditions, the changes of temperature are either continuous (the change of E_{env}
117 immediately affects the organisms) or punctuational (the intrinsic continuous change of E_{env} manifests
118 itself with probability P_m per generation, see Figs. 1b and 2b for $P_m = 0.1$).

119 The size of the populations of both plastic and elastic species are independently density-
120 regulated by a turbidostatic mechanism (Flegr, 1994). Namely, the probability of the death of an
121 individual, P_u , is $k_4 N^2 + k_5$, where k_5 is the probability of dying due to senescence or due to accident
122 (density-independent component of mortality), N is the number of individuals of a particular species,
123 and k_4 is the probability of death due to a density-dependent process, e.g., due to contracting a directly
124 transmitted parasite, the event probability of which increases with the square of N (Flegr, 1997). In our
125 simulation experiments, we set $k_4 = 5 \cdot 10^{-9}$ (which corresponds to a maximum equilibrium population
126 10 000), and $k_5 = 0.1$. The phenotype of each individual is characterized by a single parameter E ,
127 reflecting its body temperature (and therefore also indirectly the optimum temperature to live in). In
128 each generation, any individual can either die (with probability P_u), reproduce (with probability P_n), or
129 do nothing (with probability $1 - P_u - P_n$). When a particular organism reproduces, its descendant either
130 inherits the parental phenotype E or (with probability $P_x = 0.1$) mutates, i.e., its E increases or
131 decreases by 0.05. The probability of reproduction of a member of plastic and elastic species is

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$$134 \quad P_{np} = k_1 (1 - k_2 |E - E_{env}|^{m_2})$$

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$$140 \quad P_{ne} = k_1 (1 - k_2 |E - E_{env}|^{m_2} - k_3 |E - E_{orig}|^{m_3}),$$

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143 respectively. The probabilities of reproduction were bounded – when it would fall below 0, it is reset
144 to 0. k_1 is the probability of reproduction under ideal conditions, i.e., when the temperature optimum of
145 a particular individual corresponds to the actual temperature and this temperature corresponds to the
146 temperature existing at the time of the origin of the species $E = E_{env} = E_{orig}$. k_2 and m_2 characterize the
147 penalty for the deviation of the phenotype of an individual from the current temperature E_{env} , i.e., for E
148 $\neq E_{env}$, and k_3 and m_3 characterize the penalty (paid by elastic species only) for the deflection of the
149 current phenotype of an individual from the original phenotype (Flegr, 2013). In our model, the $E_{orig} =$
150 $E_{env} = 0$ at the start of our simulation experiment, and the penalty was positively correlated with the
151 squared difference between E and E_{orig} . The existence of this second penalty is the only difference
152 between elastic and plastic species, and this part of the equation is responsible for the elastic nature of
153 evolutionary responses of sexual species. In the presented simulations, we set $k_1=k_2=1$, $k_3=0.6$,
154 $m_2=m_3=2$.

155 In the present model, the low evolvability of one of the competing species was ensured by
156 introducing a penalty for the deviation of the phenotype of an individual from its original phenotype.
157 We can imagine, for example, that adapting the body temperature to a value that better corresponds to
158 the new environmental conditions could decrease the amount of energy needed for thermoregulation.
159 However, it could also impair the functions of thousands of enzymes adapted to the original body
160 temperature. The evolutionary passivity of a species could also be ensured, for example, by setting its
161 mutation rate to 0; however, such a model is not biologically realistic. In contrast, the evolutionary
162 elasticity of real species that is based on penalization for the deviation of the phenotype of an
163 individual from its original phenotype has been supported by both theoretical models and empirical
164 data, for review see (Flegr, 2010).

165

166 ***Implementation of the model***

167 The model is programmed as a modular web application in the PHP language. The parameters are
168 entered via a web form. At the start of the simulation, the time series of E_{env} is computed in AWK, the
169 interpreted programming language that can use nearly any function for computing time. The computer
170 time demanding part of the program, namely the individual-based simulation of population processes,
171 are written in C. Numerical results are visualized using gnuplot. The web application for the
172 simulation of competition that can show 1) the course of one simulation experiment and 2) aggregate
173 results for N repeated simulation experiments performed with the same parameters is available at
174 <http://fyzika.ft.utb.cz/eng/index.php>.

175 ***Procedure***

176 Three hundred individual simulation experiments were performed for all combinations of amplitude
177 and period (or pseudoperiod for aperiodic changes) for all 4 models (A : 20-980, step 60, T : 0.8-4.0).
178 Each run was terminated after 10,000 generations or when one of the species went extinct. The
179 numbers of plastic species and elastic species extinctions was compared with a two-sided Pearson's
180 Chi-squared test (goodness of fit test). The parameter space was divided into four areas as shown in
181 figures 3-7: the green area where the evolutionarily elastic species wins significantly more often ($p <$
182 0.05), the red area where the evolutionarily plastic species wins significantly more often, the gray area
183 where the difference in both species surviving was not significant, and the white area where both
184 species usually survive until the end of the simulation experiment, i.e., for 10,000 generations.

185 **Results**

186 We studied the extinction times of evolutionarily plastic and evolutionarily elastic organisms under
187 conditions of both periodically (Fig. 1) and aperiodically (Fig. 2) changing environments. Under both
188 conditions, the result of competition depended on the rate of changes and on the magnitude of the
189 changes.

190 The results of the simulation for continuous periodic changes showed that under conditions of
191 moderately-sized changes, or under conditions of rapid changes, the elastic species won significantly
192 more often than the evolutionarily plastic species. On the other hand, the evolutionarily plastic species
193 won when the changes were slow and the size of change was large, see Figs. 3-7. The evolutionarily
194 plastic species also won in a second small region of the period-amplitude parameter space, namely for
195 the periods 10-130 and the amplitudes 2.9-3.1, see Figure 7.

196 For the combination of parameters used in our simulation, aperiodic conditions favored plastic
197 species for amplitudes larger than 1.5, compare Fig. 3 and 5. In contrast, discontinuous changes (Fig. 4
198 and Fig. 6) somewhat favored the elastic species. The size of the elastic species-winning area of the
199 period-amplitude parameter space was slightly larger and its position and shape differed (see the
200 Discussion).

201 **Discussion**

202 Our results confirmed that, under fluctuating environmental conditions, the evolutionary passivity of
203 species with low evolvability, namely their limited ability to respond to selection, could provide them
204 with an advantage when competing with more evolvable species in a broad area of parameter space.
205 Under such conditions, the evolutionarily passive species had a lower risk of extinction. This
206 advantage was slightly higher when the environmental conditions fluctuated periodically and
207 discontinuously.

208 At face value, this result might seem rather counterintuitive. In our model, the members of the
209 evolutionarily passive (in our model elastic) species differed from the members of the evolutionarily
210 plastic species only by the existence of a penalty that they had to pay for a deviation of their
211 phenotype from the phenotype that they had at the start of each simulation run. Specifically, the size of
212 the penalty (a decrease of the probability of reproduction in a particular time step) was directly
213 proportional to the square of this deviation. Due to this term, the evolutionarily passive species
214 responded to selection pressure elastically and therefore only partially. It could adaptively respond to
215 small changes in environmental conditions, but not to large ones.

216 The elastic species expressed lower risk of extinction than the plastic species in a part of
217 parameter space (the green area) because the population of the plastic species adapted from time to
218 time to transiently changed conditions and it was not able to readapt quickly enough when the
219 conditions returned to or overshot the norm. On the contrary, the phenotype of members of
220 evolutionarily elastic species did not deviate from their original phenotype too much. Carriers of
221 “adaptive” mutations were rewarded for the phenotype that was better suited to their actual
222 environment. However, at the same time they were penalized for deviation of their phenotype from its
223 original status (from the phenotype that they had immediately after speciation in real species and from
224 the phenotype that they had had at the beginning of the simulation runs in our “in silico” conditions).
225 The sharp boundary between the green and red areas around the amplitude 1.5 existed for all but very
226 quickly periodically changing environments because the elastic species can survive only for a very
227 short time once E minus E_{orig} is greater than about 1.5 – for larger differences, the mean birth rate is
228 always smaller than the mean death rate. When the environmental changes were periodical and
229 continuous, the elastic species outperformed plastic species in a broad interval of rate of environmental
230 change (periods 100-860) when the size of environmental changes was relatively small (amplitude 1.1-
231 1.5), and also when the size of environmental changes were moderate and large (the amplitude 1.5-2.8)
232 and the rate of changes was large, namely the period was in a relatively narrow interval 100-180. In
233 the later part of the elastic species-winning area (the green high periodicity tail) the mean phenotype of
234 the plastic species increased or decreased strongly and settled down rather close to one of the
235 boundaries of the fluctuation interval. In contrast, the mean phenotype of the elastic species did not
236 change and remained close to E_{orig} . In consequence, the plastic species had slightly larger fluctuations
237 in abundance, which sooner or later led to its extinction. Under conditions of aperiodic and also
238 discontinuous changes, the green high periodicity tail of the elastic species-winning area was absent.
239 In the white area of no statistical difference above the green tail, the fluctuations of the plastic species
240 were too small to cause extinction, so both species survived. In the grey area, both species went extinct
241 very quickly and did not survive the first environmental fluctuation. The evolutionarily plastic species
242 usually won in slowly changing environment, especially when the changes were large (amplitudes >

243 1.6). In periodically fluctuating environment, the amplitude that was most favorable for the plastic
244 species was about 1.6, and the resistance to the increase of the amplitude raised with the size of the
245 period, i.e., the plastic species significantly outperformed the elastic species when the rate of change
246 was slow enough, e.g., when the period was at least 980, even when the amplitude was as large as 4.
247 Optically, the size of the main part of the plastic species-winning area is large. However, it must be
248 emphasized that in this region both species usually go extinct during the first period of environmental
249 change (the elastic species earlier). It is therefore questionable how (or whether) this combination of
250 parameters is biologically relevant. The plastic species also won when the changes were very fast (the
251 period or pseudoperiod was 10-110) and the size of changes was large but not maximum (amplitude
252 2.9-3.1), Fig. 7. Under these conditions, the carriers of adaptive mutations outperformed other
253 members of plastic (and also elastic) species; however, the number of carriers of standard phenotypes
254 remained relatively high at the moments when the environmental conditions returned. This probably
255 saved the plastic species from extinction. In the red bulk of this smaller part of the plastic species-
256 winning area, the phenotypes of both species were close to E_{orig} . Both populations declined rapidly and
257 fluctuated at a low level. Typically, the population of the plastic species was a bit smaller and
258 vanished first. In the left-sided tail of the red bulk (e.g. for $A = 2.7$, $T = 10$), mean phenotypes of both
259 species varied very little. Population sizes both increased and then decreased in synchrony, but the
260 elastic species usually went extinct a little bit earlier than the plastic one. It probably happened when
261 the mean phenotype of the elastic species finally changed a bit, either due to selection or due to drift
262 when the population size decreased to a very low value. When the conditions fluctuated aperiodically,
263 the amplitude most favorable for the plastic species was > 1.8 ; for these amplitudes, the plastic species
264 outperformed the elastic species even when the rate of change was very large (pseudoperiod > 20).

265 During all simulations, the evolutionarily plastic species outperformed and therefore
266 outnumbered the elastic species most of the time. However, in rarely occurring situations, e.g., when
267 the conditions changed unusually strongly and rapidly in a non-periodically fluctuating environment or
268 when many adaptive mutants appeared unusually early in a periodically fluctuating environment, the
269 plastic species was reduced to zero or to a very small value. In very small populations, genetic drift
270 (i.e., chance), rather than fitness, determines the destiny of individuals. Also, the number of arising
271 mutations is too low there. Therefore, any small population, including the population of plastic
272 species, loses the ability to adaptively respond to changes in its environment.

273 It is important to emphasize that we modeled the competition of two species that did not
274 directly interact ecologically, for example, two species that did not exploit any common resource or
275 that lived in separate areas. When, for any reason, the population of the first species increased
276 (decreased), the situation of the second species was not influenced by this. Therefore, the subject this
277 study are macroevolutionary or macroecological phenomena, namely the sorting of species or

278 populations on the basis of stability (stability-based sorting), rather than intrapopulation phenomena.
279 In principle, we modeled a situation in which plastic and elastic species were introduced 300 times to
280 two identical isolated islands and then counted how many times each species survived longer on its
281 private islands. If direct competition was permitted, e.g., when growth of the populations of both
282 species is affected by the same parasite ($P_u = k_d (N_p + N_e)^2$), the result of our simulation was different.
283 Under such conditions, the plastic species outperformed the elastic species in the whole parameter
284 space (results not shown). Competition without any direct ecological interaction operates in many
285 groups of organisms. For example, genetically different lineages of parasites as well as different
286 parasitic species rarely meet in one host even during situations when they live in the same area
287 (Morand, Poulin, Rohde, & Hayward, 1999). The same also holds for species that exploit various
288 temporary habitats like forest openings, puddles, rotting fruits or animal and plant remains. Indirect
289 competition, however, also plays an extremely important role in species with “normal” ecology. Over
290 long timescales, most habitats on Earth are unstable. Particular localities come and go, old localities
291 turn uninhabitable for particular species and new inhabitable localities originate. When a species
292 colonizes a new suitable locality, its population is at least transiently liberated from its competitors.
293 Frequently, on long-term time scales, the species that are weak direct competitors can win when they
294 are able to quickly colonize new suitable locations and there produce many new colonists before their
295 stronger competitors arrive and outcompete them, or before their locations cease to exist. Actually, the
296 low growth rate of weak competitors can be the very reason for their final victory because it can help
297 them to escape overexploitation of their resources, which can help them to keep their environment
298 (e.g. the host organism in the case of parasitic species) inhabitable for a longer time.

299 When not only rapid fluctuations but also some slow and systematic (unidirectional) change
300 occurs in a particular environment in the real world, and when the plastic species succeeds in
301 surviving the fluctuations long enough, the plastic species would finally win over its elastic
302 competitor. The penalty paid by elastic species for its out-of-date phenotype grows with the systematic
303 change of the environment until it turns incompatible with the survival of the species. Before it
304 happens, however, the elastic species could speciate, and the new species could transiently turn plastic
305 and therefore acquire the ability to adapt to changed conditions (Carson, 1968; Flegr, 2010; Mayr,
306 1954; Templeton, 2008). After such an “evolutionary reset”, the new species returns to elasticity (by
307 slow accumulation of genetic polymorphism, especially by the accumulation of mutations with a
308 frequency-dependent effect on fitness). The new elastic species will probably outcompete the old and
309 obsolete elastic species (Pearson, 1998), and the competition between the plastic species and new
310 elastic species can continue (Flegr, 2013).

311 In comparison with real systems, our model favors the plastic species in two important
312 aspects. First, in real organisms, the fitness of an individual is determined by several traits rather than

313 just one as it is in our model. Moreover, each trait is usually determined or influenced by many genes,
314 the effects of which are often not additive (Griffiths & Neumann-Held, 1999). In such a
315 multidimensional adaptive landscape, the rapid adaptation of plastic species to the drastic (rapid and
316 large) changes of an environment is probably much more difficult than in the unidimensional adaptive
317 landscape that is the subject of our simulations. The difficulty of quick return to the original phenotype
318 probably grows with the number of dimensions, and it is even possible that the plastic species could
319 finish trapped, or at least transiently trapped, in a certain location of the adaptive landscape (Schwartz,
320 2002).

321 Second, in real systems, the evolutionary passivity and elasticity of species is mostly the
322 consequence of their sexual reproduction. Therefore, in sexual species, evolutionary passivity is
323 accompanied by the persistence of a large amount of genetic polymorphism that can be sustained in
324 the population by various mechanisms related to sex (Burger, 1999; Waxman & Peck, 1999). For
325 example, in sexual species, the fixation of genotypes adapted to local conditions and the extinction of
326 locally maladapted genotypes is very slow or even impossible due to segregation and recombination,
327 as well as due to gene flow, the hybridization of members of a local population with migrants (Dias &
328 Blondel, 1996; Haldane, 1956). Moreover, sexual species can sustain their diploid status (Lewis &
329 Wolpert, 1979) and therefore can maintain a lot of genetic polymorphism in their gene pool by the
330 heterozygote advantage effect, which represents a special type of frequency dependent selection. In
331 our model, both plastic and elastic species reproduce asexually, and thus they have comparable
332 amounts of genetic polymorphism in their gene pools. Therefore, the elastic species in our model is
333 deprived of its largest advantage – the ability to very quickly (although only transiently and only
334 imperfectly) respond to rapid changes by shifting frequencies of already existing (old) alleles. In
335 contrast to a real situation, the rate of response to changes is similar in elastic and plastic species at the
336 beginning of our simulations (as it was mostly fueled by rare mutations) and slows down in the elastic
337 species as its phenotype declines from its original state. However, our present results suggest that even
338 when elastic species are stripped of this crucial advantage, they can outcompete the plastic species in a
339 broad area of parameter space. Evolutionary passivity alone, without the usually accompanying higher
340 polymorphism resulting in quicker evolutionary response to new selective pressure, can explain the
341 superiority of sexual species under fluctuating environmental conditions.

342 In our model, the elastic species was identically penalized for positive and negative divergence
343 from zero. Moreover, the environmental condition, A_{env} , fluctuated symmetrically around zero.
344 Nothing of this probably holds true in real systems. Being adapted to different than mean conditions
345 (e.g. mean temperature) strongly penalizes the elastic species, while asymmetry in fluctuation of A_{env}
346 (difference in sizes of positive and negative amplitudes, in time spent above and below zero, and in

347 rates of decreasing and increasing of A_{env}) most probably brings further advantages for the elastic
348 species in more realistic situations.

349 Typically, a positive correlation between the probability of local extinction and global
350 extinction exists (Payne & Finnegan, 2007). Therefore, a decreased probability of extinction in a
351 fluctuating environment could be advantageous not only on an ecological time scale, but also in
352 macroevolution. In agreement with the verbal arguments of G.C. Williams (1975), our results show
353 that a possible reason for the long-term success of sexual species may be, paradoxically, their lower
354 evolutionary plasticity (lower evolvability), which reduces the risk of extinction of the population or
355 species in an environment with randomly or periodically fluctuating conditions. This means that
356 sexual reproduction might not be the evolutionary adaptation that increases some aspect of direct or
357 inclusive fitness of its carriers, as it is suggested by most present theories on the origin of sex. Sex
358 could rather be the evolutionary exaptation (Gould, 2002; Gould & Lewontin, 1979) that increases the
359 chances of a given species and evolutionary lineages in the process of stability-based sorting and in the
360 process of species selection (Vrba & Gould, 1986).

361

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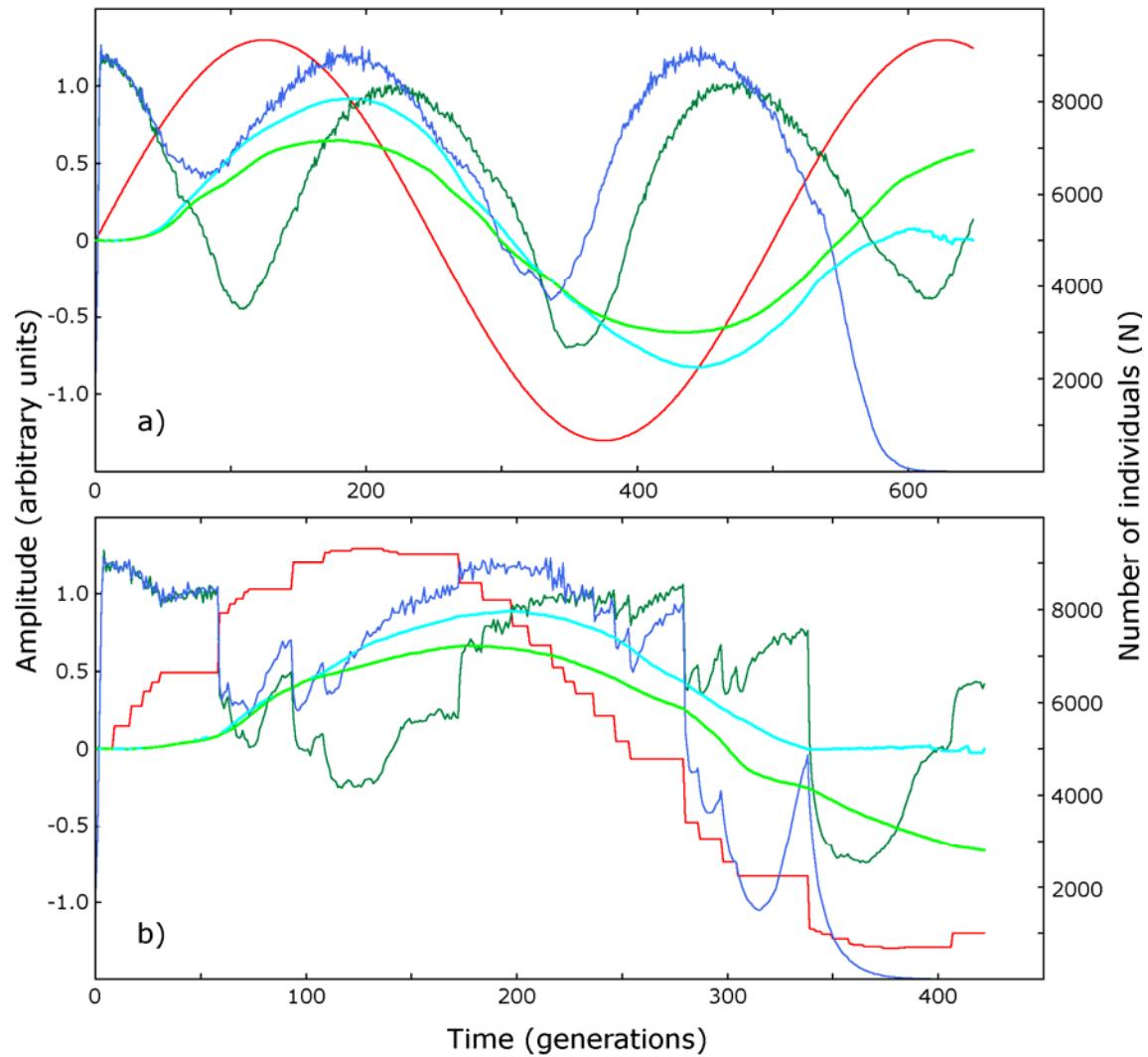
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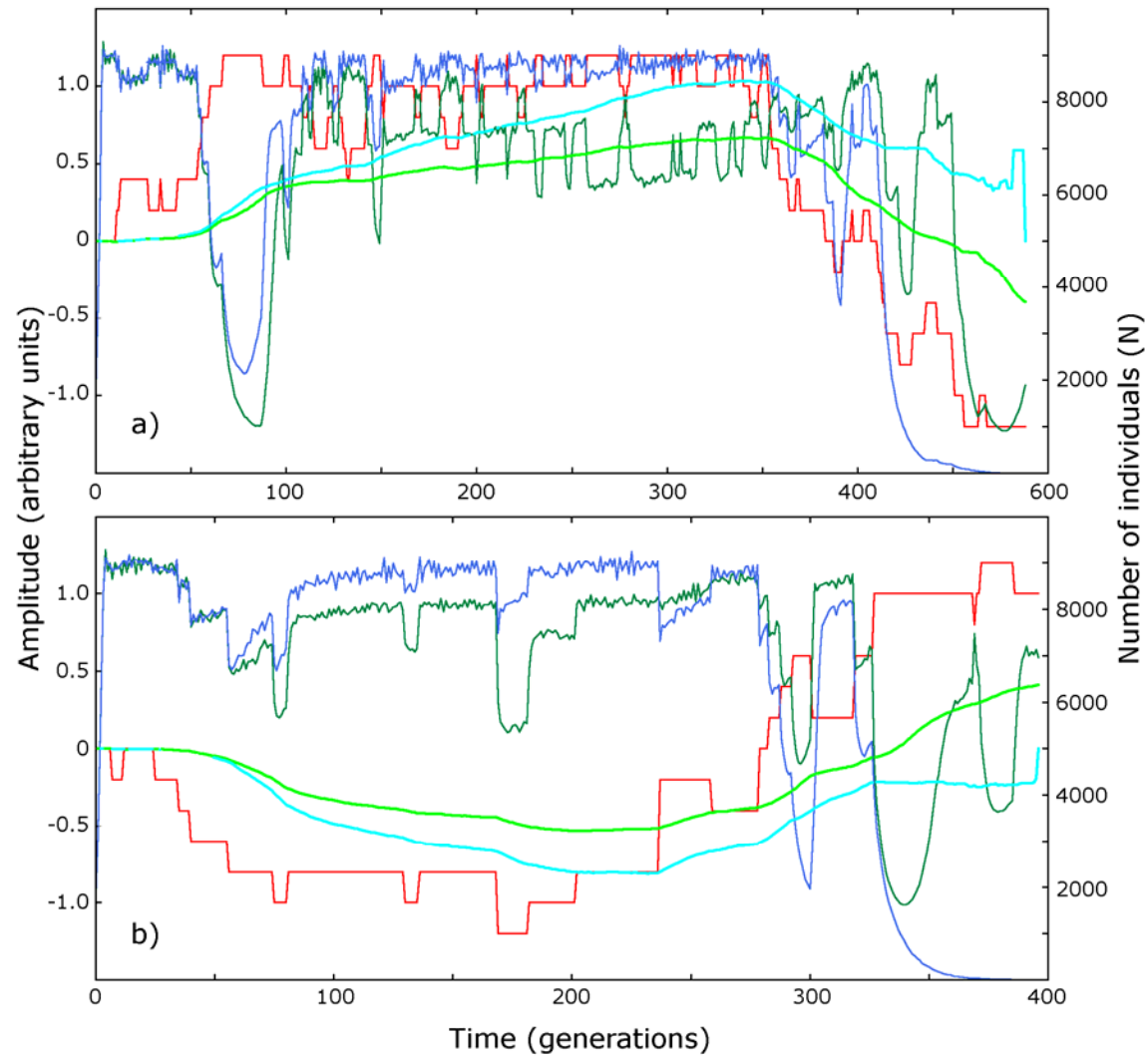
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443 Fig. 1 Competition of evolutionarily plastic and elastic species under periodically changing conditions

444 The conditions (the variable temperature - the red line) changes either continuously (the upper part
445 a) or discontinuously (lower part b). The dark blue, dark green, turquoise and light lines show the size
446 of plastic species, size of elastic species, mean phenotype (E) of elastic species and mean phenotype
447 of plastic species, respectively.

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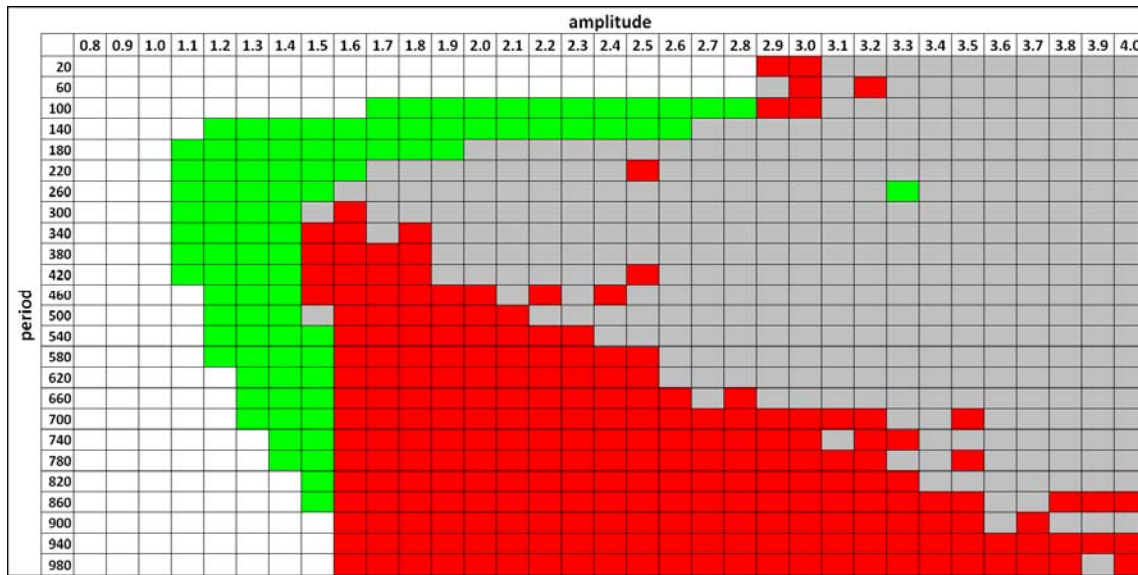
450 Fig. 2 Competition of evolutionarily plastic and elastic species under aperiodically changing
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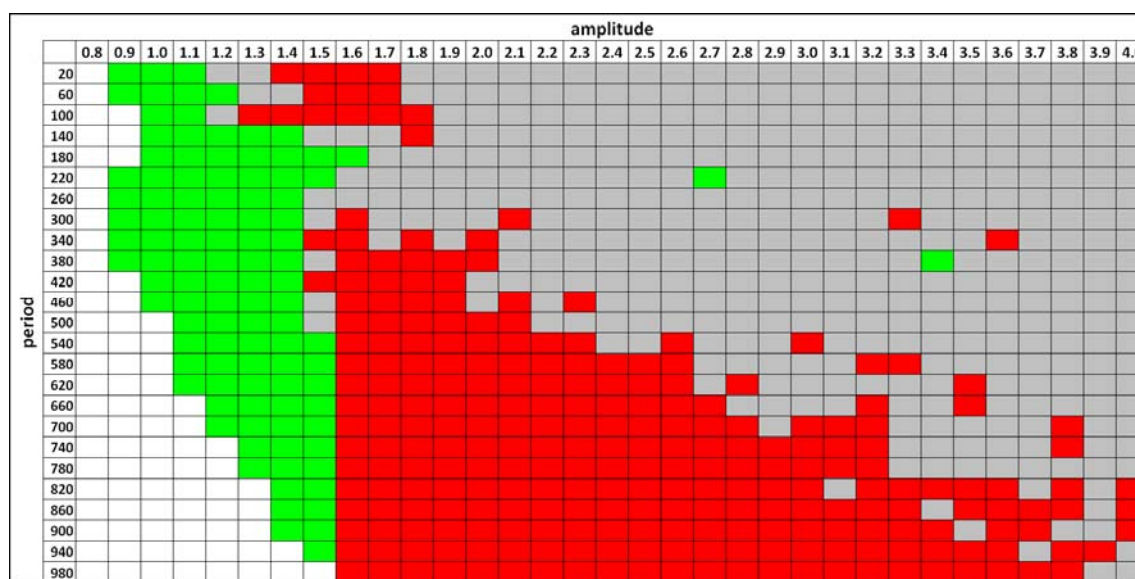
460 Fig. 3. Competition of the plastic and elastic species in various parts of the parameter space under
461 periodically and continuously changing conditions

462 The green area denote combinations of amplitude and periods of environmental changes in which the
463 evolutionarily elastic species win significantly more often (two sided goodness of fit test, $p < 0.05$),
464 the red area the combinations in which the evolutionarily plastic species win significantly more often,
465 the gray area the combinations in which the difference in survival for both species was not significant,
466 and the white area the combinations in which both species usually survive until the end of simulation
467 experiment, i.e. for 10,000 generations.

468

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470



471

472 Fig. 4. Competition of the plastic and elastic species in various parts of the parameter space under
473 periodically and discontinuously changing conditions

474 For the legend see the Fig. 3

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479 Fig. 5. Competition of the plastic and elastic species in various parts of the parameter space under
480 aperiodically and continuously changing conditions.

481 For the legend see the Fig. 3

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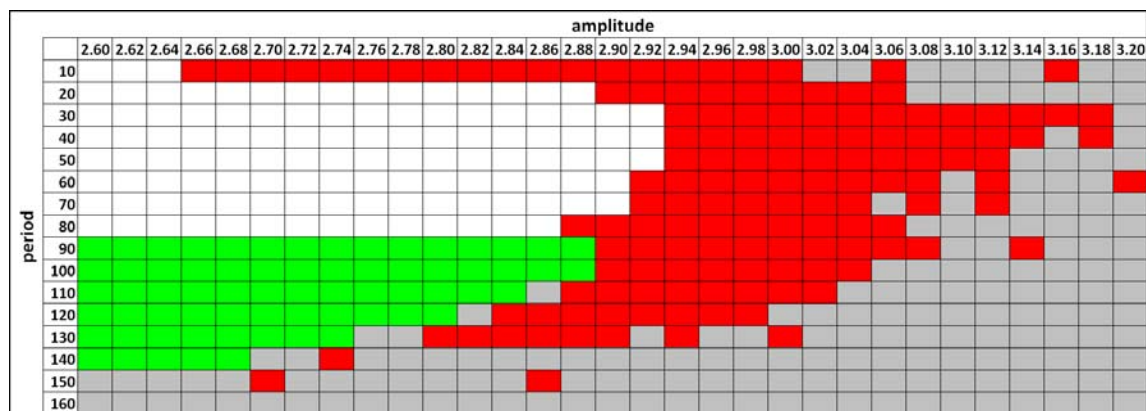
487 Fig. 6. Competition of the plastic and elastic species in various parts of the parameter space under
488 aperiodically and discontinuously changing conditions.

489 For the legend see the Fig. 3

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494 Fig. 7. Competition of the plastic and elastic species in the short period-large amplitude region of the
495 parameter space under periodically and continuously changing conditions.

496 For the legend see the Fig. 3

497

498 List of Legends

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