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

Running title: Advantages of low evolvability

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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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Introduction

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

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

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

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Methods

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 $k_4 = 5. \; 10^{-9}$ (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        $$P_{np}=k_1(1 - k_2|E - E_{env}|^{m2})$$

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137   and

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140        $$P_{ne}=k_1(1 - k_2 |E - E_{env}|^{m2} - k_3 |E - E_{orig}|^{m3}),$$

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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).

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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.

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).

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 exinction. 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 exinction, 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   wining 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 ($P_u = k_4 (N_p + N_e)^2$), 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).

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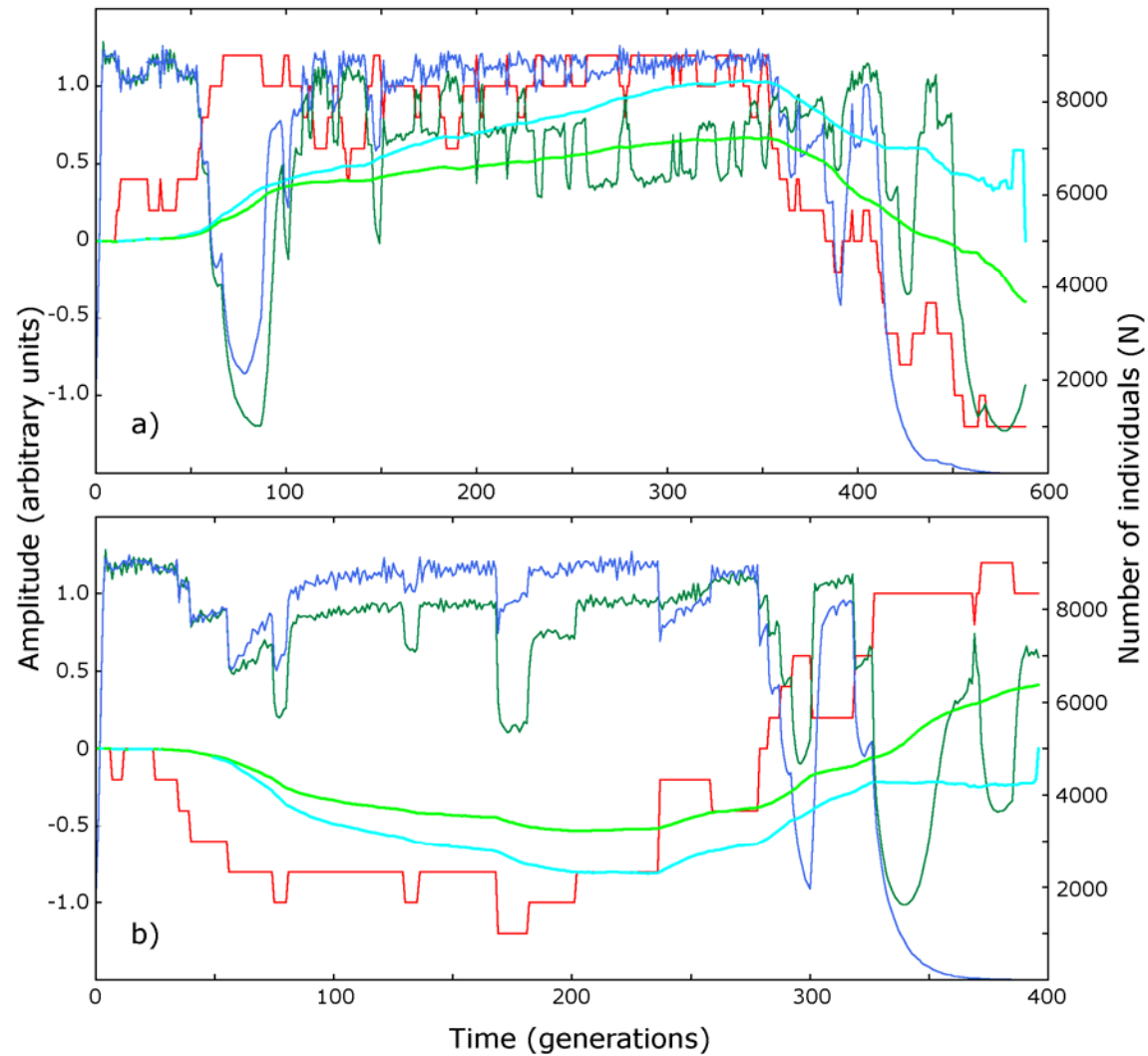
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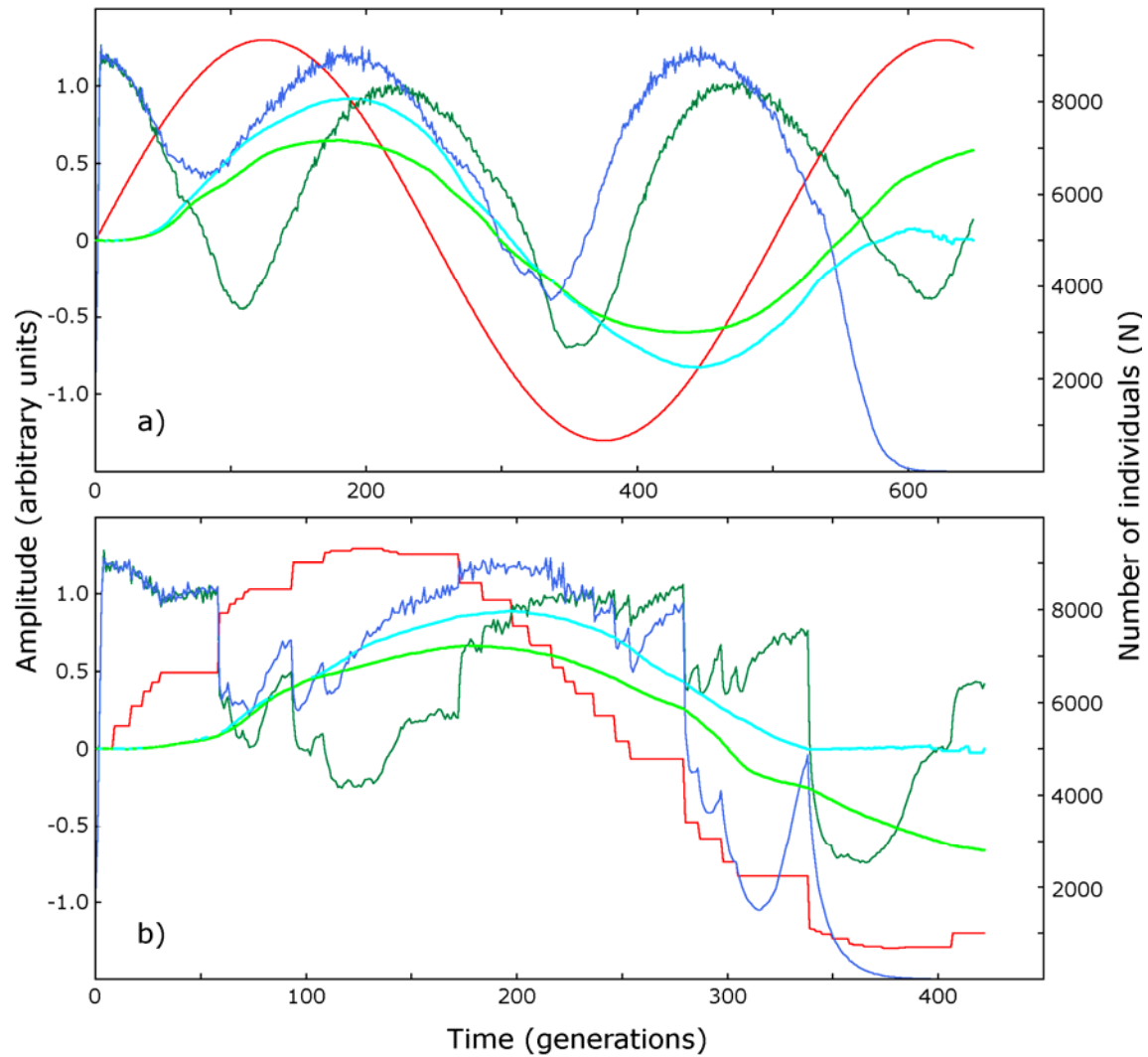
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443   Fig. 1 Competition of evolutionarily plastic and elastic species under periodically changing conditions

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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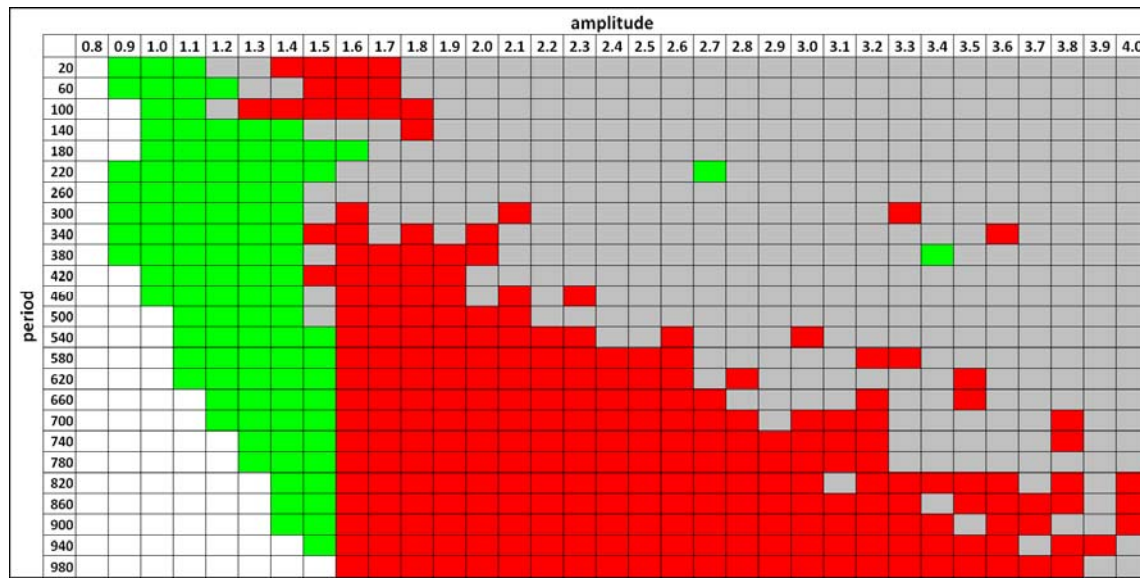
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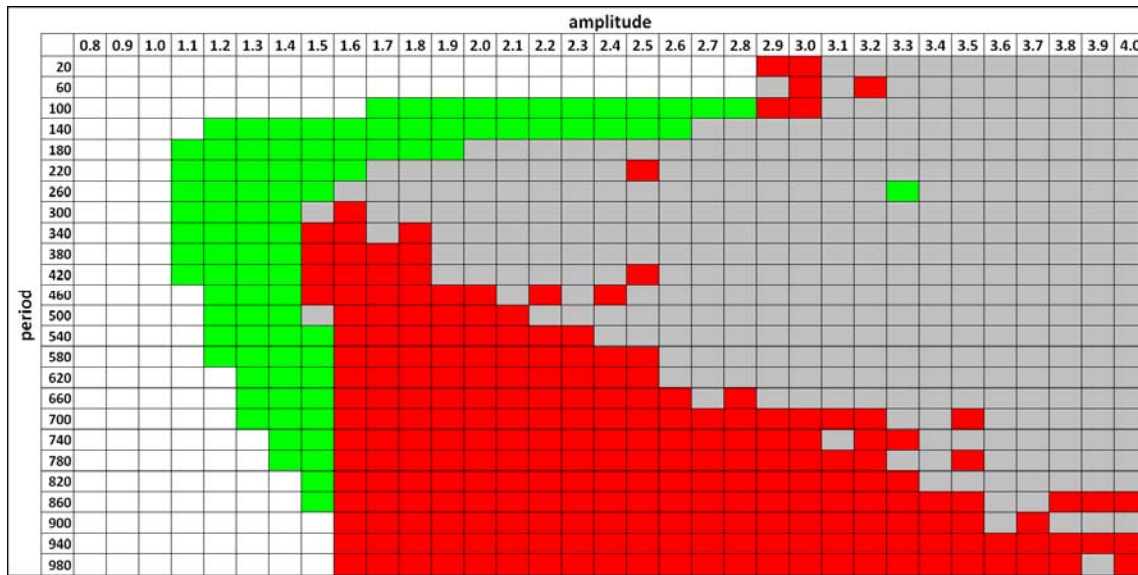
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460   Fig. 3. Competition of the plastic and elastic species in various parts of the parameter space under

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.

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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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Fig. 5. Competition of the plastic and elastic species in various parts of the parameter space under aperiodically and continuously changing conditions.
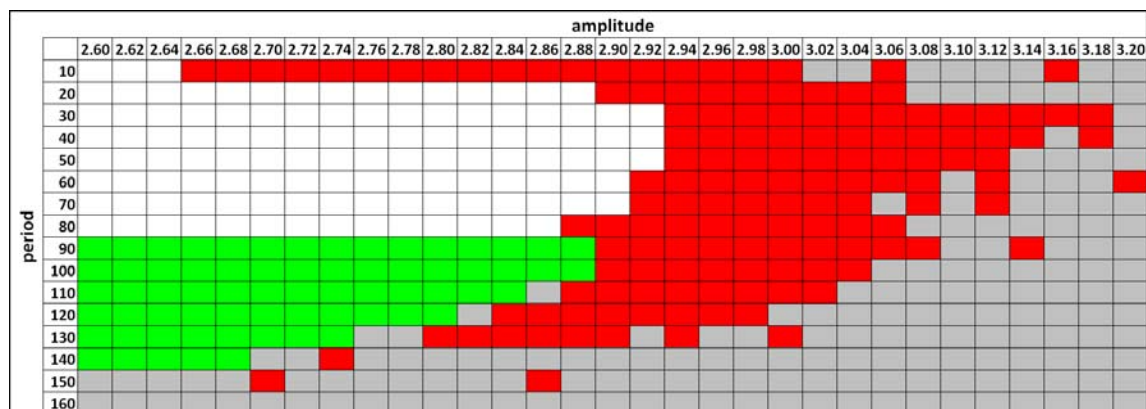
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Fig. 6. Competition of the plastic and elastic species in various parts of the parameter space under aperiodically and discontinuously changing conditions.

For the legend see the Fig. 3

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491

492

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

For the legend see the Fig. 3

497

498   List of Legends

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

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523   For the legend see the Fig. 3

524

525   Fig. 5. Competition of the plastic and elastic species in various parts of the parameter space under

526   aperiodically and continuously changing conditions.

527   For the legend see the Fig. 3

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531   For the legend see the Fig. 3

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