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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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Abstract

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

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

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

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The counterintuitive idea of Williams, which can be in fact traced back to Darwin 23319 xxx, has been theoretically studied by several authors in the context of the origin and maintenance of amphimixis, for review see (Kondrashov, 1993). The models show that under special conditions (special genetic architecture, alternating pure stabilizing and disruptive selection, etc.), the sexually reproducing organisms can outperform their asexual competitors (Gandon & Otto, 2007) 23321. However, the character of environmental fluctuation favoring low evolvability has never been studied in detail. The aim of the present study is to test the validity of the verbal models of Williams (1975) and Flegr (2013) using a numeric individual-based stochastic model. Specifically, we searched for combinations of parameters under which the inability to adaptively respond to selection alone (not in the combination with amphimixis) is advantageous and may result in the victory of less evolvable species over its more evolvable competitor. In contrast to others, we studied the behavior of a model of competition between two asexual species: the more evolvable asexual species, which can freely respond to selection (plastic species), and the less evolvable asexual species, whose members are penalized for deflecting from its original phenotype (elastic species). This allows us to distinguish whether the species overran its competitor due to its evolutionary passivity alone or due to other advantages of sexuality, such as its higher genetic polymorphism – the existence of a stock of potentially useful alleles.

Methods

Model

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

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

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

$$P_{np}=k_1(1 - k_2|E - E_{env}|^{m2})$$

and

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

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

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

Implementation of the model

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

Procedure

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

Results

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

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

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

Discussion

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

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

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

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

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

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

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populations on the basis of stability (stability-based sorting), rather than intrapopulation phenomena. In principle, we modeled a situation in which plastic and elastic species were introduced 300 times to two identical isolated islands and then counted how many times each species survived longer on its private islands. If direct competition was permitted, e.g., when growth of the populations of both species is affected by the same parasite ($P_u = k_4 (N_p + N_e)^2$), the result of our simulation was different. Under such conditions, the plastic species outperformed the elastic species in the whole parameter space (results not shown). Competition without any direct ecological interaction operates in many groups of organisms. For example, genetically different lineages of parasites as well as different parasitic species rarely meet in one host even during situations when they live in the same area (Morand, Poulin, Rohde, & Hayward, 1999). The same also holds for species that exploit various temporary habitats like forest openings, puddles, rotting fruits or animal and plant remains. Indirect competition, however, also plays an extremely important role in species with "normal" ecology. Over long timescales, most habitats on Earth are unstable. Particular localities come and go, old localities turn uninhabitable for particular species and new inhabitable localities originate. When a species colonizes a new suitable locality, its population is at least transiently liberated from its competitors. Frequently, on long-term time scales, the species that are weak direct competitors can win when they are able to quickly colonize new suitable locations and there produce many new colonists before their stronger competitors arrive and outcompete them, or before their locations cease to exist. Actually, the low growth rate of weak competitors can be the very reason for their final victory because it can help them to escape overexploitation of their resources, which can help them to keep their environment (e.g. the host organism in the case of parasitic species) inhabitable for a longer time.

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

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

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

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

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

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

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

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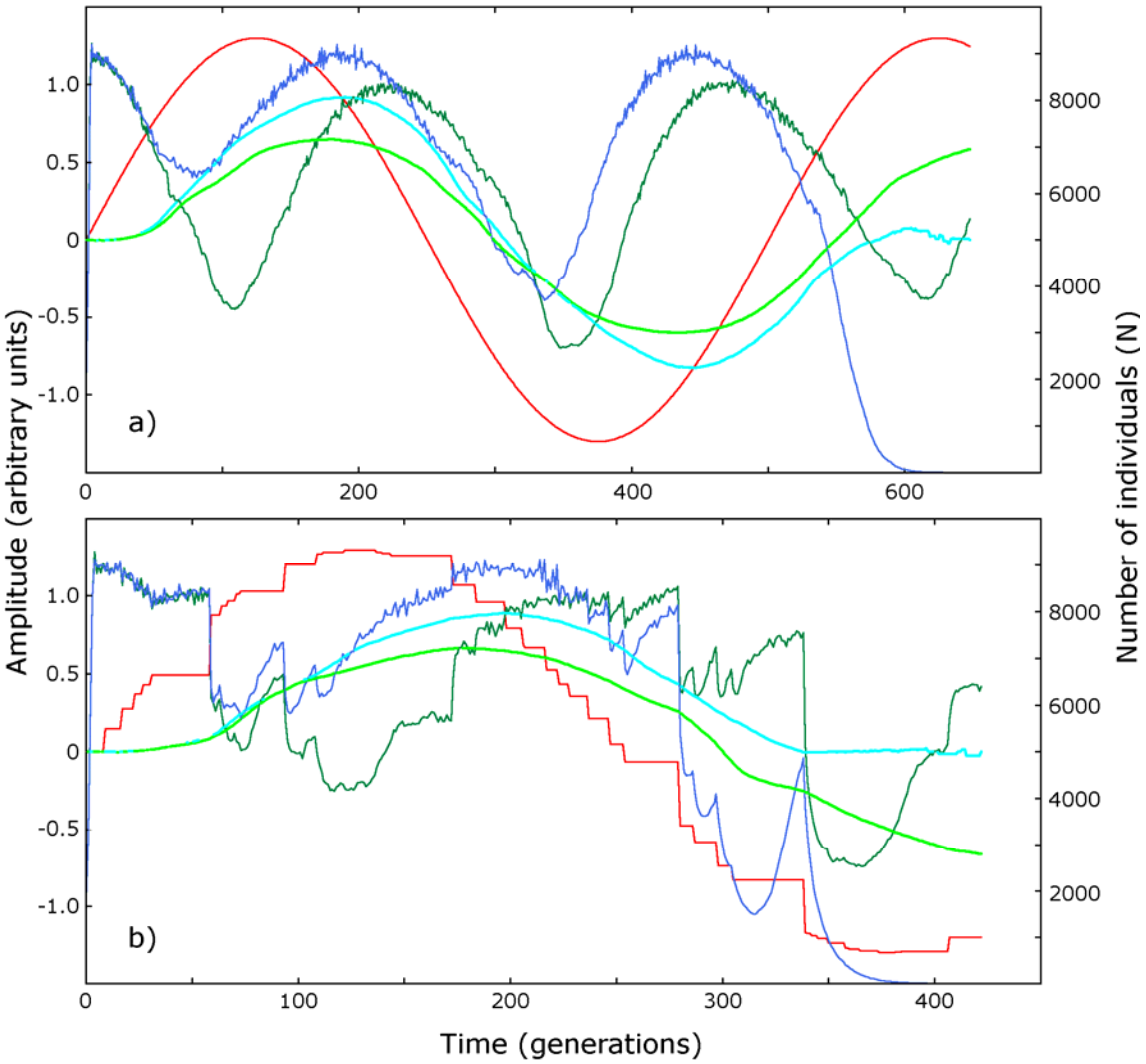

Fig. 1 Competition of evolutionarily plastic and elastic species under periodically changing conditions

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

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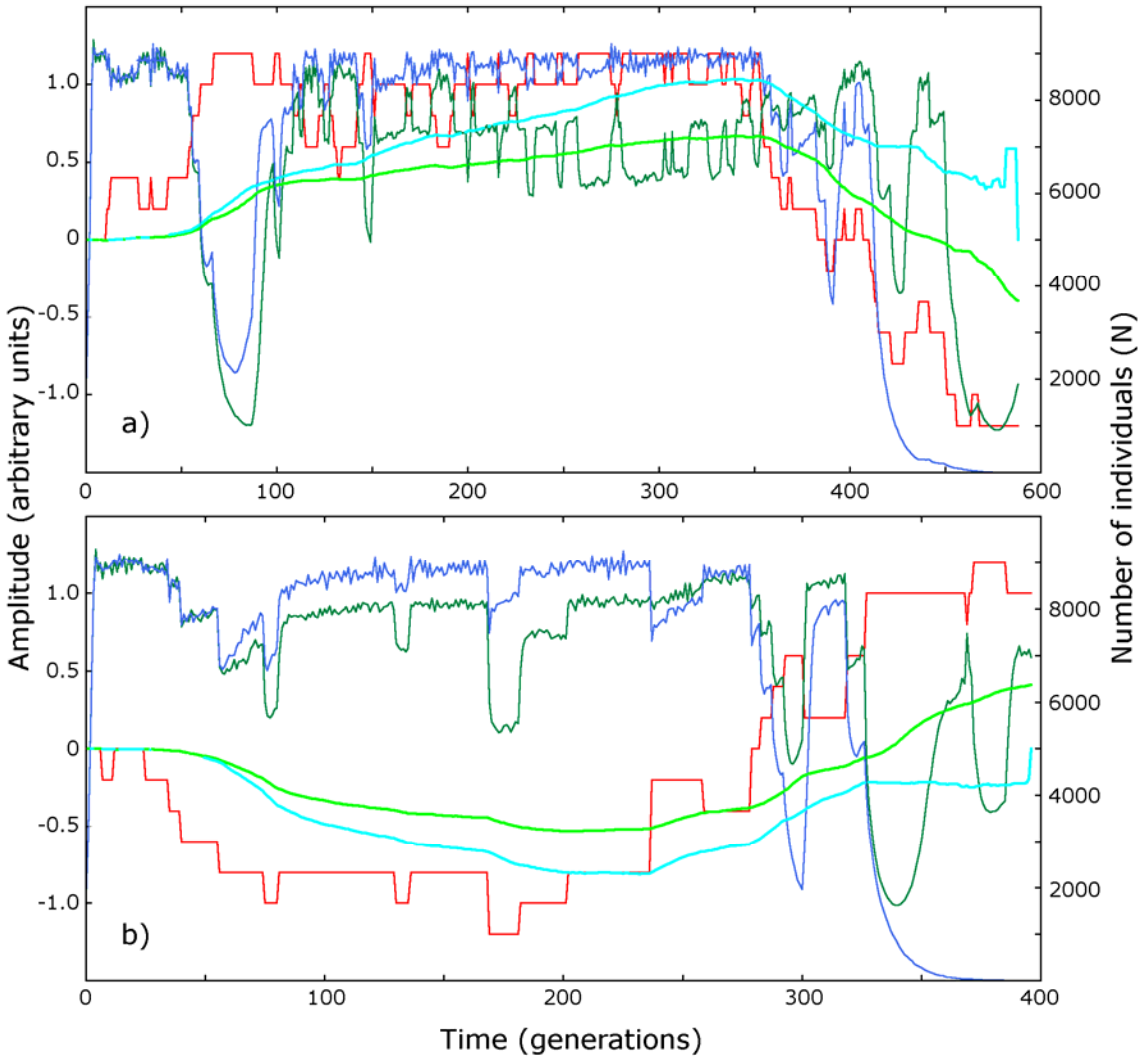

Fig. 2 Competition of evolutionarily plastic and elastic species under aperiodically changing conditions

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

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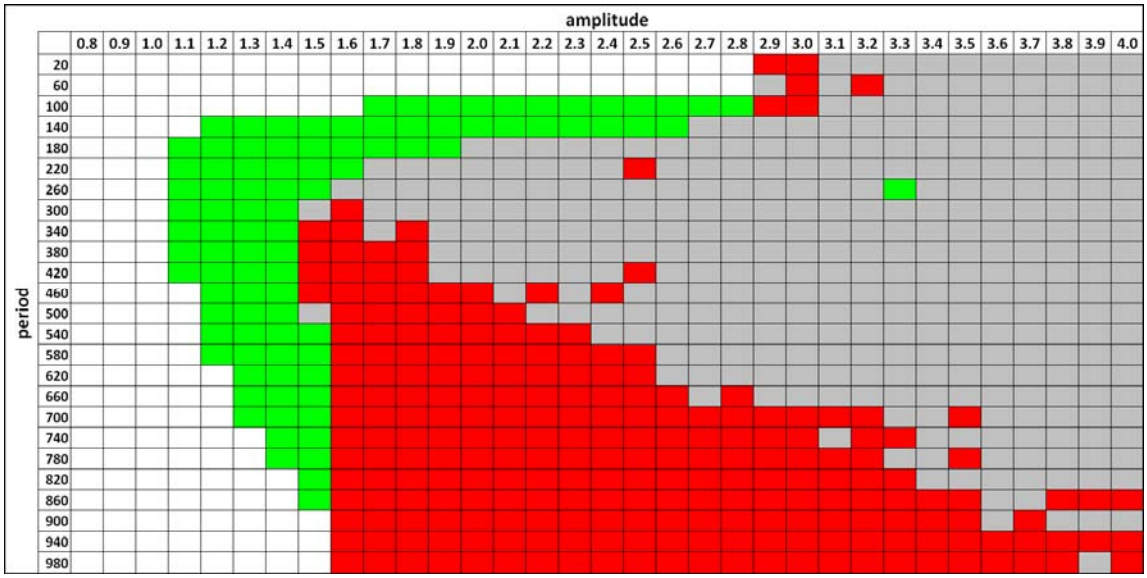

Fig. 3. Competition of the plastic and elastic species in various parts of the parameter space under periodically and continuously changing conditions

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

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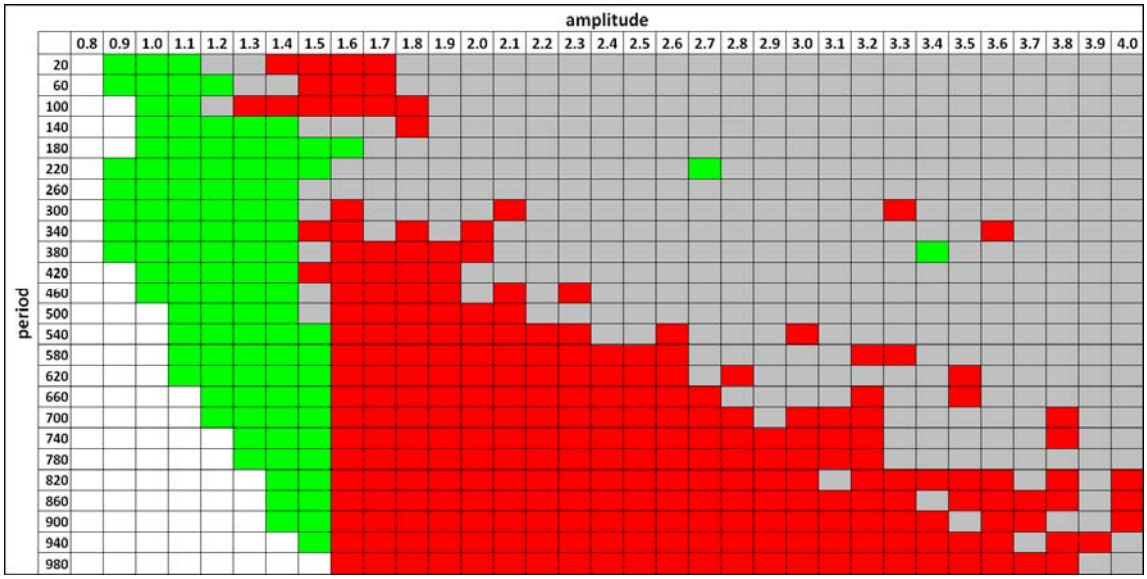

Fig. 4. Competition of the plastic and elastic species in various parts of the parameter space under periodically and discontinuously changing conditions

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.

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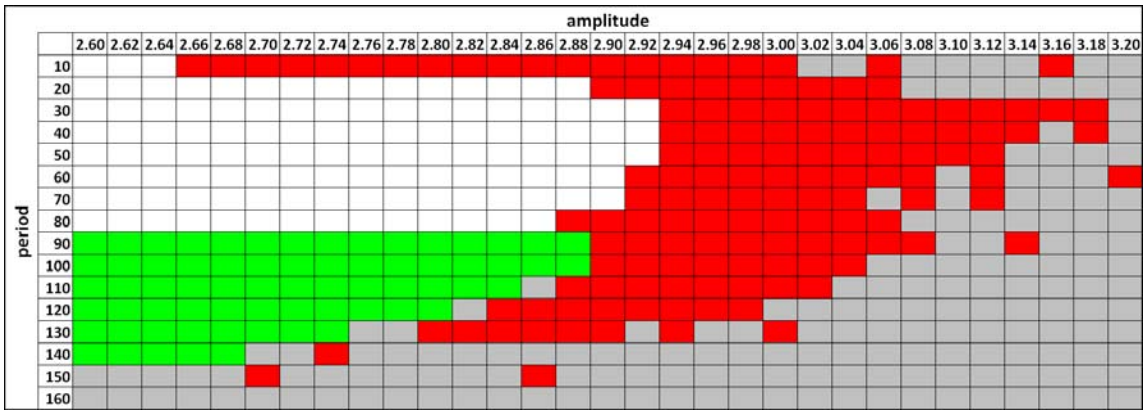

Fig. 7. Competition of the plastic and elastic species in the short period-large amplitude region of the parameter space under periodically and continuously changing conditions.

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List of Legends

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Fig. 3. Competition of the plastic and elastic species in various parts of the parameter space under periodically and continuously changing conditions

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