On the importance of being stable: evolutionarily frozen species can win in fluctuating environments

JAROSLAV FLEGR[1]* and PETR PONÍŽIL[2,3]

[1]*Department of Biology, Faculty of Science, Charles University in Prague, Viničná 7, 128 44 Prague, Czech Republic*
[2]*Department of Physics and Materials Engineering, Tomas Bata University in Zlin, Vavrečkova 275, 760 01 Zlin, Czech Republic*
[3]*Center of Polymer Systems, Tomas Bata University in Zlin, 762 72 Zlin, Czech Republic*

The ability of organisms to respond adaptively to environmental changes (evolvability) is usually considered to be an important advantage in interspecific competition. It has been suggested, however, that evolvability could be a double-edged sword that could present a 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 that differ only by their evolvability. They show that, in changeable environments, less evolvable species could outperform their more evolvable competitors in a broad area of a parameter space. Highly evolvable species prospered better nearly all the time; however, they sustained a higher probability of extinction during rare events of the rapid transient change of conditions. It explains why sexual species, with their reduced capacity to respond adaptively to local or temporal environmental changes, prevail in nearly all biotopes.

ADDITIONAL KEYWORDS: asexual species – competition – evolvability – extinction – frozen plasticity – model – origin of sex – punctuated equilibrium – sex – stability-based sorting.

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; Otto, 2009). Many models and hypotheses have been published within the past 40 years to describe the conditions in which sexually reproducing organisms can outperform their asexual competitors, including asexual mutants (Bell, 1982; Maynard Smith, 1978). For many, but not all, of these models, such as DNA repairing models (Hörandl & Hadacek, 2013) or variants of Muller's 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, obligate sex prevails in many taxa, despite the fact that theoretical studies clearly show that it is nearly always outperformed by facultative sex, i.e. 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. Owing to the effect of gene flow and the negative influence of segregation and recombination on the heritability of phenotypic traits and fitness, the ability of populations of sexual species to adapt to local 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,

*Corresponding author. E-mail: flegr@cesnet.cz;

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including alleles that are suboptimal in the present local conditions. Such alleles interfere with the ability of sexual species to adapt fully and deeply to local conditions. However, 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, including selection in favour of heterozygotes, in the sexual organisms (Flegr, 2010). Together with pleiotropy and epistasis, the presence of a certain amount (possibly not too large an 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 to respond to directional selection. One of the implications of this theory is that sexual species are favoured in randomly or periodically fluctuating environments, i.e. in most environments on the surface of Earth, owing to their lower ability to respond evolutionarily to changes in their environment. The stabilization of the composition of the gene pool by frequency-dependent selection not only prevents the population from the elimination of momentarily suboptimal alleles (Williams, 1975) but also limits its ability to respond to selection and, by doing so, protects the population against an adaptation to transient changes in its environment (Flegr, 2013).

The counterintuitive idea of Williams regarding the advantage of lower evolvability (ability of organisms to respond adaptively to environmental changes) has been studied theoretically by several authors in the context of the origin and maintenance of sexual reproduction (for reviews, see Kondrashov, 1993; Toman & Flegr, 2018). The models show that in special conditions (specific genetic architecture, alternation of stabilizing and disruptive selection, etc.), sexually reproducing organisms can outperform their asexual competitors (Roughgarden, 1991; Gandon & Otto, 2007). For example, Roughgarden (1991) showed that, in fluctuating conditions, returns of frequencies of particular phenotypes to Hardy–Weinberg equilibrium in each generation bounds the variance in the mean fitness of sexual species, which automatically results in a higher geometrical mean of fitness, and therefore better performance of a sexual species in competition with an asexual species. However, neither competition of two asexual species or two sexual species differing only in evolvability, nor the character of environmental fluctuation favouring sexuality, has ever been studied in detail.

The aim of the present study was to test the validity of the verbal models of Williams (1975) and Flegr (2013) using a numerical, individual-based stochastic model. Specifically, we searched for combinations of parameters with which a lower ability to respond adaptively to selection alone (not in combination with sexual reproduction) is advantageous and may result in the victory of a less evolvable species over its more evolvable competitor. Our study has been inspired by, and has implications for, theories of the origin and maintenance of sexuality. However, it must be emphasized that we studied not the competition of sexual and asexual species but the competition between two asexual species: a more evolvable asexual species, which can respond freely to selection, and a less evolvable asexual species, whose members are penalized for deflecting from its original phenotype. This is because the aim of present study was not to test whether sexual species outperform their asexual competitors in fluctuating conditions. It is possible that in such conditions the sexual species could overrun its competitor not because of its lower evolvability but owing to other already known advantages of sexuality, such as the capacity to select two or more positive mutations in parallel or the ability to stop Muller's ratchet. In our model of competition of two asexual species, we intentionally stripped the less evolvable species of all other potential advantages to see whether, in certain conditions, solely the lower evolvability could ensure its victory in a competition.

MATERIAL AND METHODS

MODEL

We modelled the indirect competition in resistance to extinction of two asexual species that differ only by their evolvability: the more evolvable plastic species and less evolvable elastic species. The terms 'plastic' and 'elastic', used in the present paper to distinguish two species, have been borrowed from physics. In 'plastic' organisms, the size of the change in population mean phenotype in response to constant force (constant selection pressure) is unceasing, regardless of how far the phenotype is from its original state. In the elastic species, the size of the change in population mean phenotype in response to constant force is negatively proportional to the distance of the current phenotype from its original state. At a certain distance, this response can decrease to zero, and the phenotype of the organisms stops responding to selection.

The time in our stochastic, individual-based model is discrete, i.e. all births and deaths and environmental changes happen simultaneously, and it is measured in 'seasons'. In each season, individuals propagated with a given probability and died with another probability. Therefore, each season can be considered to be one reproductive period of a species. We used this model to

study 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_{opt}, is represented by a sinusoid that is characterized by its amplitude A and period T (for the sake of clarity, the amplitude is given as (maximum – minimum)/2, not maximum – minimum; formally, it is half the 'peak-to-peak amplitude'). Figure 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 season. Here, the rate of environmental change is characterized by the pseudoperiod T (determined by the combination of ΔE and P_E), which is numerically equal to the period T of the periodic model, for which the average speed of E_{opt} change 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 $-A$). Figure 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 season; see Figs 1B, 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 $k_4N^2 + k_5$, where k_5 is the probability of dying as a result of senescence or accident (density-independent component of mortality), N is the number of individuals of a particular species, and k_4 is the probability of death as a result of a density-dependent process, e.g. as a result of contracting a directly transmitted parasite, the event probability of which increases with the square of N (Flegr, 1997). In our simulation experiments, we set $k_4 = 5 \times 10^{-9}$ (which gives a maximal equilibrium population of ~10 000) and $k_5 = 0.1$. The phenotype of
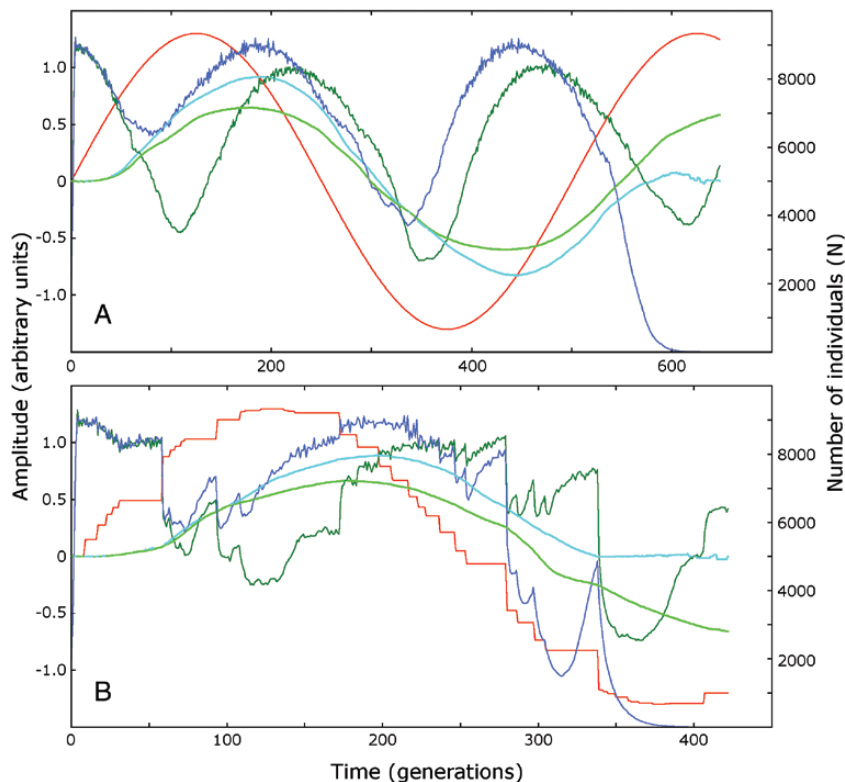
Figure 1. Competition of evolutionarily plastic and elastic species in periodically changing conditions. The conditions (variable temperature, indicated by the red line) change either continuously (A) or discontinuously (B). The dark blue, dark green, turquoise and light green lines indicate the size of plastic species, size of elastic species, mean phenotype (E) of elastic species and mean phenotype of plastic species, respectively.

each individual is characterized by a single parameter E, reflecting its body temperature (and therefore also indirectly the optimal temperature to live in). In each season, any individual can die (with probability P_u), reproduce (with probability P_n) or do nothing. 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

$$P_{np} = k_1 \left(1 - k_2 \mid E \quad E_{env} \mid^{m_2}\right) \qquad (1)$$

and

$$P_{ne} = k_1 \left(1 - k_2 \mid E \quad E_{env} \mid^{m_2} -k_3 \left| E - E_{orig} \right|^{m_3}\right), \qquad (2)$$

respectively. The probabilities of reproduction were bounded; when it fell below zero, it was reset to zero. The parameter k_1 is the probability of reproduction in 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, $E = E_{env} = E_{orig}$. Parameters 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 deviation 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 real evolutionary passive species, e.g. sexual species, i.e. for the slowing down and final stoppage of an evolutionary response of the elastic species on selection. In the presented simulations, we set $k_1 = k_2 = 1$, $k_3 = 0.6$ and $m_2 = m_3 = 2$, and for this combination of parameters the analytical solution of equation (2) shows that the elastic species will stop responding to selection at the distance $E = 0.625E_{env}$, whereas the plastic species will continue responding until $E = E_{env}$.
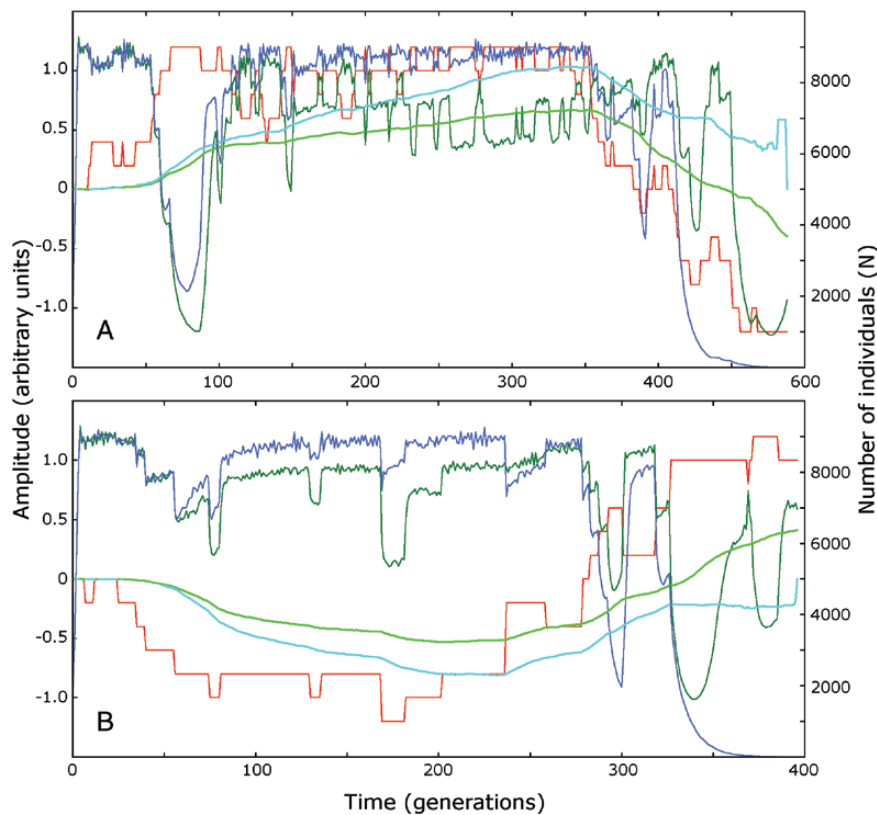
Figure 2. Competition of evolutionarily plastic and elastic species in aperiodically changing conditions. The conditions (variable temperature, indicated by the red line) change either continuously (A) or discontinuously (B). The dark blue, dark green, turquoise and light green lines indicate the size of plastic species, size of elastic species, mean phenotype (E) of elastic species and mean phenotype of plastic species, respectively.

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 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.

### 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. The computer time-demanding part of the program, namely the individual-based simulation of population processes, is 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.
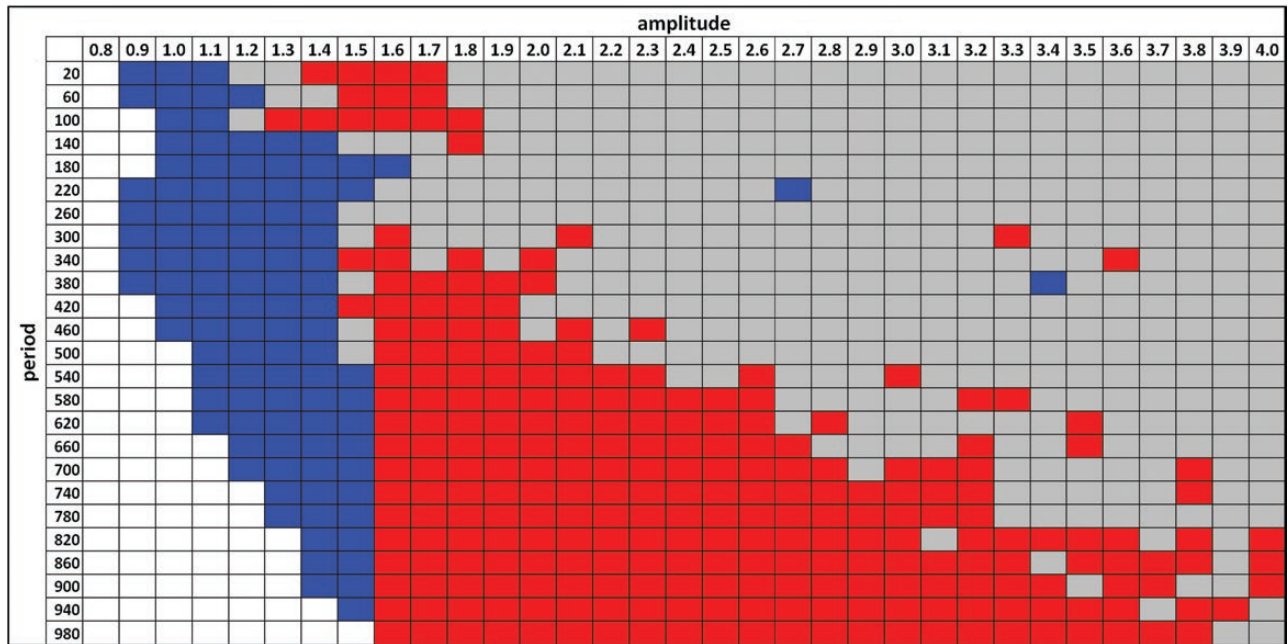
PROCEDURE

Three hundred individual simulation experiments were performed for each combination of amplitude and period (or pseudoperiod for aperiodic changes) (A, 20–980, step 60; T, 0.8–4.0). Each run was terminated after 10 000 seasons 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 χ^2 test (goodness-of-fit test). The parameter space was divided into four areas as shown in Figures 3–7: the blue 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 grey area where the difference in both species surviving is not significant, and the white area where both species usually survive until the end of the simulation experiment, i.e. for 10 000 seasons.

RESULTS

We studied the extinction times of evolutionarily plastic and evolutionarily elastic organisms in conditions of both periodically (Fig. 1) and aperiodically (Fig. 2) changing environments. In both conditions, the
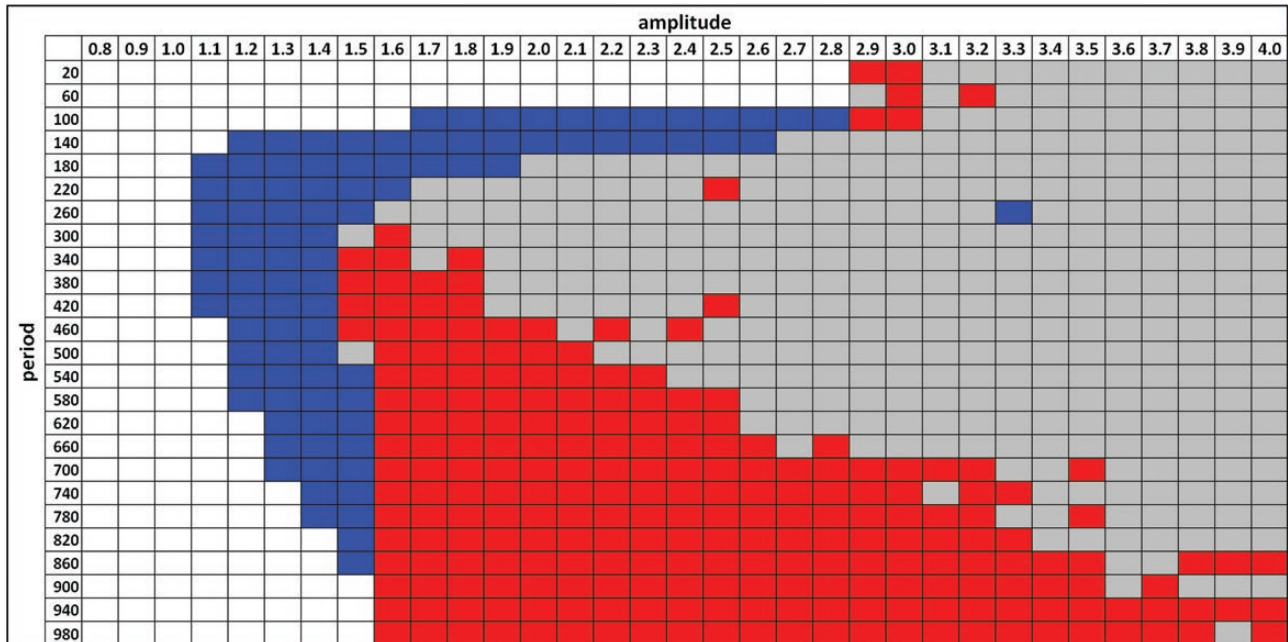
Figure 3. Competition of the plastic and elastic species in various parts of the parameter space in periodically and continuously changing conditions. The blue areas denote combinations of amplitude and periods of environmental changes in which the evolutionarily elastic species wins significantly more often (two-sided goodness-of-fit test, $P < 0.05$), the red areas the combinations in which the evolutionarily plastic species wins significantly more often, the grey areas the combinations in which the difference in survival for both species was not significant, and the white areas the combinations in which both species usually survive until the end of simulation experiment, i.e. for 10 000 seasons.

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Figure 4. Competition of the plastic and elastic species in various parts of the parameter space in periodically and discontinuously changing conditions. For explanation, see the legend to Figure 3.
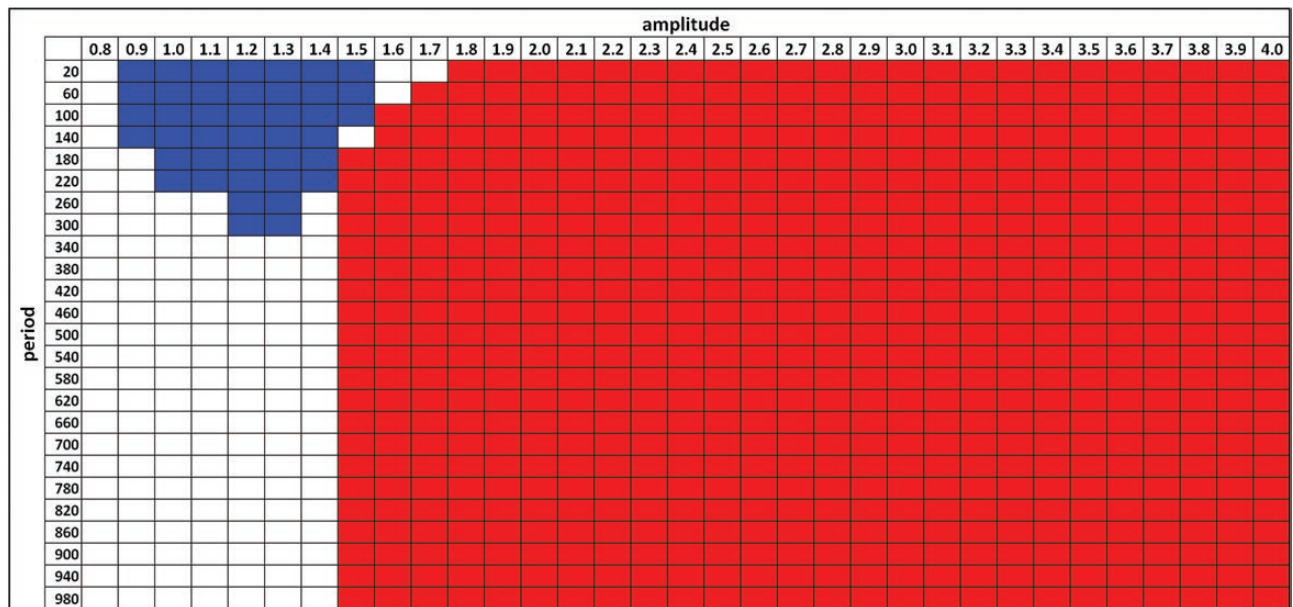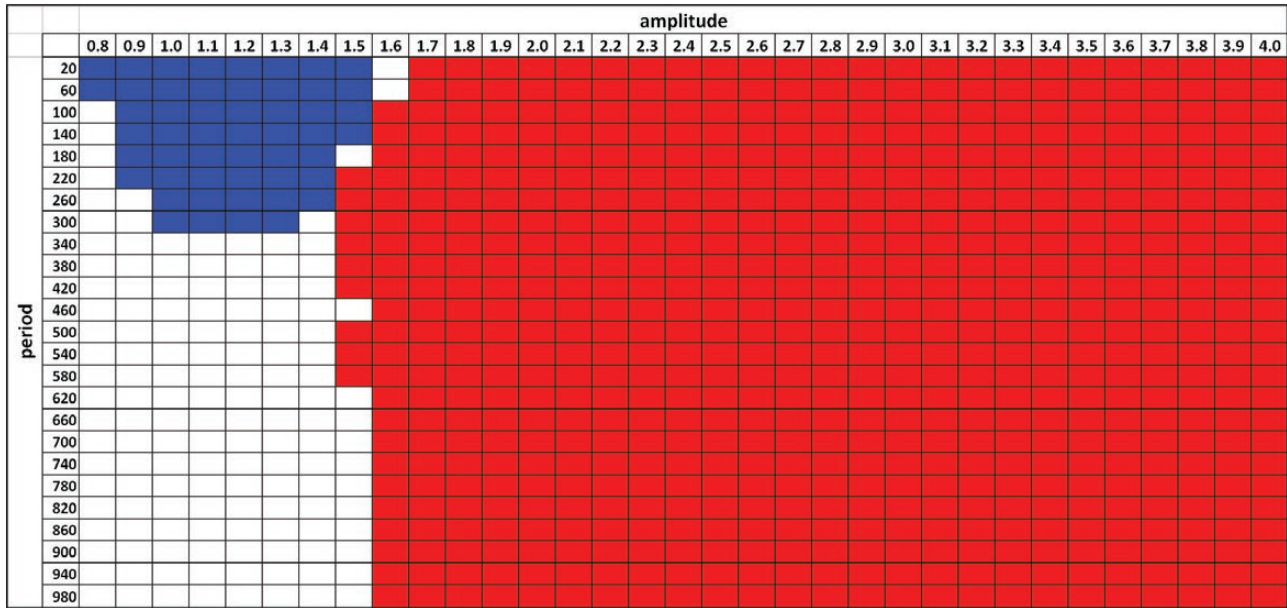

Figure 5. Competition of the plastic and elastic species in various parts of the parameter space in aperiodically and continuously changing conditions. For explanation, see the legend to Figure 3.

performance of the plastic species (measured by mean fitness or mean population size) was better most of time. However, the final result of the competition depended on the rate and the magnitude of the changes.

The results of the simulation for continuous periodic changes showed that in conditions of moderately sized changes or in conditions of rapid changes, the elastic species won significantly more often than the evolutionarily plastic species. On the contrary, the evolutionarily plastic species won when the changes were slow and the size of change was large; see Figures 3–7. The evolutionarily plastic species also won in a second

Figure 6. Competition of the plastic and elastic species in various parts of the parameter space in aperiodically and discontinuously changing conditions. For explanation, see the legend to Figure 3.
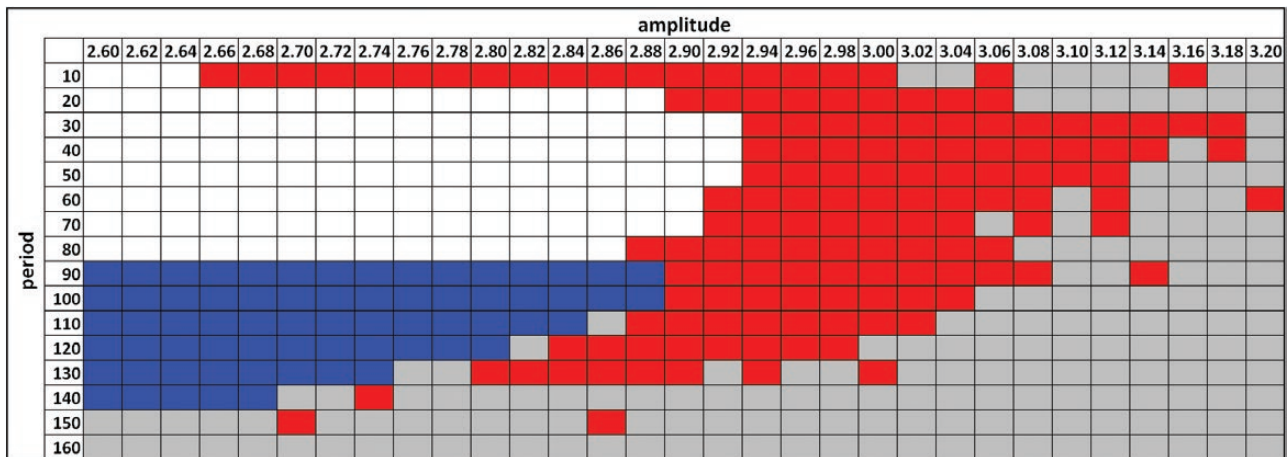
Figure 7. Competition of the plastic and elastic species in the short period–large amplitude region of the parameter space in periodically and continuously changing conditions. For explanation, see the legend to Figure 3.

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 favoured plastic species for amplitudes > 1.5; compare Figures 3 and 5. In contrast, discontinuous changes (Figs 4, 6) somewhat favoured 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, in fluctuating environmental conditions, the evolutionary passivity of species with low evolvability, namely their limited ability to respond to selection by adaptive phenotypic change, could provide them with an advantage when indirectly competing (see below) with more evolvable species in a broad area of parameter space. In 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.

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 reduction of the probability of reproduction in a particular time step) was directly proportional to the square of this deviation. Owing to this term, the evolutionarily passive species responded to selection pressure elastically (at first easily, but slowing their response in time, and stopping altogether in the end) and therefore only in part. It could respond adaptively to small changes in environmental conditions, but not to large ones.

The elastic species showed a lower risk of extinction than the plastic species in a part of parameter space (the blue area) because the population of the plastic species adapted from time to time to transiently changed conditions, not being able to re-adapt quickly enough when the conditions returned to or overshot the norm. On the contrary, the phenotype of members of the 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 the deviation of their phenotype from the phenotype that they had had at the beginning of the simulation runs. The sharp boundary between the blue and red areas around the amplitude 1.5 existed for all but very fast periodically changing environments because the elastic species can survive for only a very short time once E minus E_{orig} is > ~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 the plastic species in a broad interval of rate of environmental change (periods 100–860) when the size of environmental change 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 blue 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. In conditions of aperiodic and discontinuous changes,

the blue high-periodicity tail of the elastic species winning area was absent. In the white area of no statistical difference above the blue tail, the fluctuations of the plastic species were too small to cause exinction; therefore, 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 environments, especially when the changes were large (amplitudes > 1.6). In periodically fluctuating environments, the amplitude that was most favourable for the plastic species was ~1.6, and the resistance to the increase of the amplitude increased 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 ≥ 980, even when the amplitude was as large as four. 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 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 the maximum (amplitude 2.9–3.1; Fig. 7). In 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 winning 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. This probably occurred when the mean phenotype of the elastic species finally changed a bit, either because of selection or because of drift when the population size decreased to a very low value. When the conditions fluctuated aperiodically, the amplitude most favourable 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 underwent an unusually strong and rapid change in a non-periodically fluctuating environment or, in

a periodically fluctuating environment, when many adaptive mutants appeared unusually early during the selection period and therefore shifted the mean phenotype too far from the norm, 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 mutations arising is too low. Therefore, any small population, including the population of plastic species, loses the ability to respond adaptively to changes in its environment.

It is important to emphasize that we modelled the indirect competition of two species that did not interact ecologically; for example, two species that did not exploit any common resource or that lived in separate areas of the environment. 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 subjects of this study are macroevolutionary or macroecological phenomena, namely the sorting of species or populations on the basis of stability (stability-based sorting; Toman & Flegr, 2017), rather than microecological phenomena such as direct interspecific or intraspecific competition for resources. In principle, we modelled a situation analogous to a scenario in which plastic and elastic species are introduced 300 times to two identical isolated islands and then counted how many times each species survived longer on its own island. If direct competition was permitted, e.g. when growth of the populations of both species was affected by the same parasite $[P_u = k_4(N_p + N_e)^2]$, the result of our simulation was different. In such conditions, the plastic species outperformed the elastic species in the whole parameter space (results not shown). However, competition without any direct ecological interaction operates in many groups of organisms. For example, genetically different lineages of parasites or different parasitic species rarely meet in one host even in situations where when they live in the same area (Morand *et al.*, 1999). The same holds for species that exploit various temporary habitats, such as 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 time scales, most habitats on Earth are unstable. Particular localities come and go, old localities become 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 colonize new suitable locations quickly and there produce many new colonists before their stronger competitors arrive and outcompete them or before their locations cease to exist.

In fact, it can be speculated that the low growth rate of weak competitors could 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 certain environment, 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 the elastic species for its out-of-date phenotype grows with the systematic change of the environment until it becomes 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, as was proposed in some punctuational theories of evolution (Mayr, 1954; Carson, 1968; Templeton, 2008; Flegr, 2010). After such an 'evolutionary reset', the new species returns to elasticity (by the slow accumulation of genetic polymorphism, especially by the accumulation of mutations with a frequency-dependent effect on fitness). The new elastic species would probably outcompete the old and obsolete elastic species (Pearson, 1998), and the competition between the plastic species and the new elastic species can continue (Flegr, 2013).

Seemingly, our results contrast with results of comparative studies that mostly show that asexual species are more common in unstable environments (e.g. disturbed habitats, intertidal, temporal pools, temperate habitats) whereas sexual species are relatively more common in stable environments, e.g. in the tropics (Bell, 1982). It is necessary to reiterate that we studied the competition of a more evolvable asexual species with a less evolvable one, not the competition of asexual with sexual species. Also, we did not compare the performance of these two species in more stable and less stable environments, but in environments that differed by the nature of their changes, by the combination of their amplitudes and frequencies. Figures 3–7 clearly show that it is not possible to say which species is better adapted to rapidly or slowly fluctuating environments; it always depends on the amplitude of the environmental change. Finally, yet importantly, the results of recent comparative studies performed exclusively on ancient asexual species, the species that successfully passed the test of long-term (> 1 Myr) persistence in nature, showed that whenever the environment of asexual species differed from the environment of its related sexual species, the asexual species lived in a less heterogeneous environment (Toman & Flegr, 2018).

In comparison with real systems, our model favours the plastic species in two important ways. First, in real organisms, the fitness of an individual is determined

by several traits rather than only 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 rapid 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 (Roughgarden, 1991; Bürger, 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 owing to segregation and recombination, in addition to gene flow, i.e. the hybridization of members of a local population with migrants (Haldane, 1956; Dias & Blondel, 1996). Moreover, on a large time scale, sexual species can sustain their diploid status, whereas diploid or polyploid asexual species will finely turn functionally haploid owing to the accumulation of mutations in spare copies of genes (Lewis & Wolpert, 1979). Owing to their diploidy, they can maintain high 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 (as shown by the similar standard deviation of E in outputs of our program). Therefore, the elastic species in our model is deprived of its largest advantage, i.e. the ability very quickly (although only transiently and only imperfectly) to respond to rapid changes by the 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 (because it was mostly fuelled by rare mutations) and slows down in the elastic species as its phenotype declines from its original state. Nevertheless, 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 therefore explain the superiority of sexual species in fluctuating environmental conditions.

CONCLUSIONS

Typically, a positive correlation exists between the probability of local extinction and global extinction (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 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 is suggested by most present theories on the origin of sex. Instead, sex could be the evolutionary exaptation (Gould & Lewontin, 1979; Gould, 2002; Casinos, 2017) 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; Toman & Flegr, 2017).

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