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Microevolutionary a macroevolutionary implication of Frozen plasticity theory of adaptive evolution

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Summary

According to theory of frozen plasticity, adaptive evolution in sexual species operates just after the birth of a species by peripatric speciation – while it is still evolutionary plastic. Most of the time, i.e. 98-99% of a species duration (as estimated on the basis of paleontological data) sexual species are evolutionarily elastic on a microevolutionary time-scale and evolutionarily frozen on a macroevolutionary time-scale and can only passively wait for such changes in their environment that cause either their extinction, or for the highly improbable event of a return of a part of the population to the plastic state due to peripatric speciation. Here I show that the frozen plasticity theory has a large number of evolutionary and ecological implications. Most of these predictions could be tested empirically, and should be analyzed in greater depth theoretically. The frozen plasticity theory, which includes the Darwinian model of evolution as a special case – i.e. the evolution of species in a plastic state, not only offers many new predictions to be tested, but also provides explanations for a much broader spectrum of known biological phenomena than classical evolutionary theories.

Introduction

The mechanism of natural selection can easily explain the evolution of adaptive traits amongst asexually reproducing organisms where genotype and fitness is regularly and fully inherited from parent to offspring. Amongst organisms that reproduce sexually, the genotype of the individual is formed in each generation through the random mixing of the genes of the two parents and thus the genotype and fitness of individuals is not fully inherited, which complicates adaptive evolution by means of natural selection. The selfish gene theory was proposed in the 1970's to explain the functioning of adaptive evolution amongst sexually reproducing organisms. According to this theory, individuals do not compete for the greatest fitness within a population, but rather the alleles compete in the framework of a single locus for the ability to transfer the greatest number of their copies into the gene pool of the next generation. However, this theory neglects the fact that the effect of the individual alleles on the phenotype, as well as the effect of the individual phenotype traits on the fitness of individuals, depends on the other alleles that are present in the genotype of the individual. The theory of evolutionarily stable strategies indicates that, under such conditions, selection pressures cannot lead to long-term changes in the phenotypes of organisms, but only to a deflection of the frequency of the individual alleles from equilibrium. The greater this deflection, the more the gene pool resists this pressure; after the cessation of selection pressure, the frequency of the alleles spontaneously returns to their original values. The theory of frozen plasticity^(1,2) suggests that sexually reproducing species can respond evolutionarily to selection pressures (they are evolutionarily plastic) only when members of that particular species are genetically uniform, i.e. only after a portion of the population of the original species has split off, balanced on the edge of extinction for several generations, and then undergone rapid multiplication. Following a short period of time, estimated on the basis of paleontological data to correspond to 1-2% of the duration of the species, genetic polymorphism accumulates in the gene pool; and thus, in each generation, new mutations occur in the presence of different alleles – the species ceases to behave in an evolutionarily plastic manner and becomes evolutionarily elastic on a microevolutionary time-scale and evolutionarily frozen on a macroevolutionary time-scale. It then exists in this state until such time as such changes accumulate in the environment that the evolutionarily frozen species becomes extinct.

Here I show that the frozen plasticity theory has a large number of evolutionary and ecological implications. Most of these predictions could be tested empirically, and should be analyzed in greater depth theoretically. I will show that the frozen plasticity theory, which includes the Darwinian model of evolution as a special case – i.e. the evolution of species in a

plastic state, not only offers many new predictions to be tested, but also provides explanations for a much broader spectrum of known biological phenomena than classical evolutionary theories.

Frozen Plasticity Theory and Microevolutionary Processes

Microevolutionary processes are the evolutionary processes operating on the level of populations or individual species. In microevolution, the species or population has to respond to relatively rapid abiotic and biotic changes in its environment. Therefore, the source of evolutionary novelty in microevolution is the genetic variability already available in the population; this is to say, it is geared by gene flow, rather than the slow processes of the generation of new and useful alleles by mutagenesis.

The theory of frozen plasticity and classical theories of adaptive evolution differ in many of their predictions. The most important difference is that according to the classical theory, all species respond to selection as though they were plasticine, they respond in a plastic way; while according to the frozen plasticity theory, 98-99% of species respond to selection as though they were rubber, they respond in an elastic way. At first, they readily respond to selection pressure; however as the average phenotype of the organism deviates from its original state, selection is less and less effective and, at a certain point, the population stops responding to it. When the selection stops, the average phenotype of the population members returns to the original state.

There are several critical implications of the evolutionary elasticity of species. In the world of elastic species, organisms are not optimally adapted to the conditions of their current environment but to those present during the evolutionary plasticity of that particular species. This should hold especially for evolutionarily old species, as their environmental conditions probably differ most from those existing at the time of their origin. For example, algae originated in the Paleozoic, when days lasted about 21 hours, and are known to better synchronize their circadian rhythms with shorter light-dark cycles than the current 24-hour cycle⁽³⁾.

Representatives of old, macroevolutionarily frozen, microevolutionarily elastic species that are kept out of their original state by natural selection, have lowered fitness (viability or fertility) in comparison with representatives of young species living under conditions similar to those existing at the time of their origin. Therefore, statistically, the population density of a species probably negatively correlates with species age; a study of the correlation of the molecular age of a species with their average abundance could easily test this prediction. This could also explain the existence of the most universal ecological law – that every community shows a hollow curve on a histogram with many rare species and just a few common species⁽⁴⁾. The position of a species on

the histogram is rather stable; species retain their basic status as common or rare as long as one million years⁽⁵⁾. The frozen plasticity theory predicts that the common species are the young species which are still evolutionarily plastic or which have only recently lost their plasticity and are therefore still adapted to current environmental conditions. This is in agreement with the observation that the correlation between global and local abundance only exists in young but not in old species. Probably, old species are not able to compete with other species in as broad a spectrum of biotopes as are young species⁽⁶⁾. The frozen plasticity theory also predicts that in the paleontological record, gradual change from common to rare species would be more likely than the opposite change from rare to common species.

It can also be expected that populations near the center of the geographical range of a species express higher mean fitness than those near the borders of the range, which have had to adapt to conditions different from those existing at the site of the most probable origin of the species – the center of the range. For example, it has been observed that tits are able to adapt to a different climate, with its corresponding shift in the peak abundance of caterpillars, by a shift of their own breeding season. However, the fertility of these adapted populations of tits decreases in comparison with birds adapted to the original climate^(7,8).

Species elasticity and the negative correlation between deviation from the equilibrium frequency of alleles (and from the original phenotype of the species) and fitness could also provide an alternative explanation for the very existence of distinct geographic ranges of species. Elastic species can adapt to geographically changing conditions only to a certain degree. At some point, the decrease in fitness accompanying both the departure from the phenotype as well as that of allele frequency from the original state is so sharp that it is incompatible with the long-term survival of the population. The same negative correlation between departure of phenotype and allele frequency from the original state and mean fitness could explain the lower viability and fertility of most decorative breeds of practically any species of domesticated animals.

Unsurprisingly, when the populations of pure-bred animals are left to their fate, members of the given population return to the original phenotype of their wild predecessors within a few generations. This phenomenon differs from the return of the phenotype of an original wild form in the case of crosses between two different races. In crosses, the almost immediate return to the original phenotype is caused by a breakdown of the unique combination of alleles (responsible for the appearance of the members of the individual races) as a consequence of recombination and segregation of alleles. In members of the same race, there is a gradual return to the original wild phenotype as a consequence of the action of natural selection which, during a few subsequent generations, removes from the population the individuals with reduced viability and fertility, i.e.

with the phenotype of the race bred by humans.

The elasticity of most sexual species could also explain the long-term coexistence of species that use the same resource. Theoretical analysis shows that such coexistence is possible, but highly unstable in evolutionarily plastic species⁽⁹⁾. Sooner or later, one of the plastic species increases in intensity or efficiency the exploitation of a limited resource, thereby causing the extinction of the competing species. The absence of evolutionary plasticity in sexual species could be an important positive factor in the conservation of global and local biodiversity.

The low and vanishing inheritance of phenotypic traits in polymorphic sexual species could also explain the persistence of altruistic behavior and general efficiency of group selection. The most serious objection of evolutionary biologists against the role of group selection in evolutionary processes consists in the fact that a trait that provides an advantage to a group and simultaneously places the individual that is its carrier at a disadvantage has a low chance of spreading and enduring in nature. Groups in which the altruistic trait spreads would prosper better than groups in which this trait is lacking and the average fitness of the members of this group would be greater; however, selfish individuals who do not exhibit this trait and do not behave altruistically, but only enjoy the advantages provided by the presence of altruists, would have the greatest fitness within these groups. In sexual (frozen) species, any behavioral trait (for example, altruistic behavior) is usually determined by the greater number of genes and many of these genes have (due to epistasis) a context-dependent influence on the particular trait. Consequently the heritability of most traits is low. Under such conditions, altruists emerge from the population as if by chance in families that are completely unrelated and have different phenotypes, i.e. individuals with quite different behavior, with a probability that is determined only by the proportion of particular alleles in the entire population. Thus populations can compete for the greatest average fitness of their members; those that have the greatest proportion of the relevant alleles, resulting in the greatest number of altruists being formed (emerging by chance), will win in this competition. Thus, group and inter-species selection can occur in nature in favor of altruistic traits (because the percentage proportion of alleles in the population is inherited from one generation to the next) and its results cannot be cancelled out by individual selection because the trait itself, altruistic behavior, is not inherited.

The existence of two types of species, a very common frozen (elastic) species and a very rare plastic species, offers a new explanation for the existence of invasive species, the species that for whatever reason spread from their originally limited range into new areas. The transfer of a species to a new territory (by man or otherwise) is generally a necessary condition for invasion, but is still not a sufficient condition. In the vast majority of cases, the species succumbs to

competition with the local species and dies out. Only a small fraction of introduced species is “successful”. For example, red deer (*Cervus elaphus*) were introduced to New Zealand a total of 32 times and only the last attempt was successful; but these deer now occupied the entire area of the southern island⁽¹⁰⁾. Similarly, the now excessively successful starling (*Sturnus vulgaris*) settled in America only after at least nine attempts⁽¹¹⁾. The spread of a successful species is usually preceded by a relatively long lag phase, in which the to-be-invasive species peacefully coexists with the native species in the limited area of their original introduction.

According to classical evolutionary theories, the native species, which are adapted to local conditions, should outcompete newcomers^(12,13). According to the frozen plasticity theory, the ecological success of some newcomers is not so surprising. During the introduction and following lag phase, the genetic polymorphism of an introduced population decreases, which could result in the conversion of a frozen species to the plastic state⁽¹⁴⁾. Frozen species are best adapted to the conditions existing at the time of their origin (past conditions) while plastic species can adapt to current conditions. Moreover, plastic species can outcompete frozen species in the coevolutionary arm race. Data on the evolutionary plasticity of invasive species are rather scarce⁽¹⁵⁻¹⁷⁾; however in certain species, e.g. invasive grass *Phalaris arundinacea*, a higher heritability and higher evolutionary plasticity (larger response of the phenotype of the grass to local conditions) were demonstrated in North America than in its original area in Europe⁽¹⁸⁾. In an accord with this prediction of frozen plasticity theory, the parthenogenetic⁽¹⁹⁾ and polyploid⁽¹⁷⁾ species are overrepresented among invasive species.

The existence of only a low fraction of evolutionarily plastic species can also explain the fact that man succeeded in domesticating only a negligible number of plant and animal species⁽²⁰⁾. Only plastic species can adapt to the drastically changed conditions of life in captivity without significant decreases in viability and fertility. The frozen plasticity theory suggests that domestication should be successful mostly in young species, which have not yet had enough time to freeze. It is worthwhile to remember that most selection experiments were performed either on domestic animals, with probably lower genetic variance from the very beginning,⁽²⁰⁾ or on small populations that had passed a strong bottleneck just before, or at the beginning of, the experiment. Therefore, the ability of a species to respond to selection is probably overestimated and that of natural elasticity underestimated by the results of such experiments or of long-term selection programs performed on domesticates⁽²¹⁾.

As for domesticated plants, the frozen plasticity theory predicts that most varieties would have been derived from species with the capacity for vegetative reproduction, e.g. by means of tubers, rhizomes or grafts, or from self-pollinating species⁽²⁰⁾. The frozen plasticity theory argues

that the plasticity of species with asexual reproduction is comparatively higher than those with sexual reproduction, and plasticity is higher in self-pollinating species than in cross-pollinating species. Therefore, these species can be more easily changed by artificial selection. On the other hand, sexually reproducing and cross-pollinating varieties should be more stable and lose their useful properties acquired originally by artificial selection more slowly. Due to natural selection, a plastic variety has a tendency to increase its fertility at the expense of properties useful for man. In contrast, a sexually reproducing (elastic) variety can only respond to natural selection to a certain degree, and therefore cannot lose its useful properties due to natural selection. It was reported in the older literature that the varieties of cross-pollinating rye usually remained in seed company catalogues much longer than did those of self-pollinating wheat⁽²²⁾.

The plasticity of asexually reproducing species should be better off in an environment, in habitats, poor in resources or where the survival of most species is limited over a long period of time by unfavorable abiotic factors. Here, the main criterion of evolutionary success is how well (not how quickly) the species can change its phenotype in response to the requirements of the environment. It is noteworthy that asexually reproducing species or asexually reproducing lineages of otherwise sexually reproducing species of plants and animals are found primarily in habitats with extreme conditions – in habitats that are extremely dry, extremely cold or extremely poisonous. The proportion of asexual species increases, for example, with increasing altitude and latitude or in places where the soil contains high concentrations of poisonous heavy metals^(23,24). On the other hand, sexually reproducing (elastic) species should be better off in an environment rich in resources and with many competing species where the rate of evolutionary responses in the coevolutionary arm-race plays the crucial role. The fact that they could retain most of their genetic polymorphism enables them to rapidly respond to any evolutionary pressure by shifting frequencies of their alleles without needing to wait for rare advantageous mutations.

Evolutionary elasticity of sexual species could also be advantageous in a long-term perspective. Under fluctuating conditions of a stochastic environment, a plastic asexual species could adapt to a transient environmental change while an elastic sexual species resists such change of its phenotype. When the environmental conditions return to normal, the plastic species could fail to return to its optimal phenotype quickly enough and is therefore at risk of extinction, while the population of an elastic species is able to return to its original phenotype within a few generations. As was already suggested by G.C. Williams⁽²⁵⁾, the main advantage provided by sexual reproduction could consist in a substantial reduction in the evolutionary ability of most species. As a consequence of their elasticity, sexually reproducing species are evolutionarily passive throughout much of their existence and cannot opportunistically (i.e. without regard to

future negative consequences) respond to temporary short-term changes in external conditions.

Frozen Plasticity Theory and Macroevolutionary Processes

Macroevolutionary processes operate on a higher level than that of species and on a much longer time scale; therefore even the very slow process of origination of new alleles by mutation could play the part of source for evolutionary novelty. In contrast to microevolutionary processes, macroevolutionary processes, such as speciation or species selection, i.e. the competition of phylogenetic lineages for higher rates of speciation and lower rates of extinctions, usually do not result in the origin of evolutionary adaptations. Therefore, the characteristic result of macroevolution is an increase in biological disparity (accumulation of new body plans) rather than improvement of old or origin of new adaptive traits. Chance, rather than deterministic processes like selection or evolutionary drives, probably plays a key role in macroevolution (for an opposite opinion on the role of chance in evolution see⁽²⁶⁾).

According to the theory of frozen plasticity, sexual species behave as elastic in microevolution processes and as frozen in macroevolutionary processes. They respond to minor environmental change with reversible change (accompanied by decrease in fitness) and to major environmental change with extinction rather than with evolutionary adaptation. The most important difference between the predictions of the classical evolutionary theories and frozen plasticity theory can be summarized as follows: according to the former, there should be no correlation between cladogenesis and anagenesis (between speciation and changes in the phenotype of organisms) while the latter assumes that the irreversible phenotypic changes are always associated with speciation. The opposite does not hold as most speciation events such as vicariant allopatric speciation, parapatric speciation and many forms of sympatric speciation (with the exception, for example, of speciation by polyploidization and the accompanying transition from sexual to asexual reproduction) are not coupled with a dramatic reduction in genetic polymorphism and return to plasticity. These forms of speciation could be responsible for the origin of most species, while new genera or higher taxa (i.e. the monophyletic lineages with characteristic evolutionary novelties) mostly result from peripatric speciation. Therefore, the frozen plasticity theory predicts that the amount of evolutionary changes in a phylogenetic lineage reflects the number of speciations in this line rather than its age. These two parameters often correlate with each other; however, the modern multivariate statistical techniques allow testing the effects of these two parameters separately. A study in passerine birds has found the number of speciation within a phylogenetic line to have a very strong positive effect on the rate of

anagenesis. The number of species alone explained 33.3% of the total variation in morphology⁽²⁷⁾. Moreover, the reported rate of anagenesis on islands seems to be higher than on the mainland. The higher frequency of peripatric speciation on islands than on the mainland can be the clue to the observed phenomenon.

The positive correlation between the rates of anagenesis and speciation can be detected even on the molecular level. A molecular study⁽²⁸⁾ has shown that a relatively large part of the variability in the substitution rate can be explained by differences in the speciation rate between evolutionary lineages. Of course, a large part of the monitored nucleotide substitutions are neutral mutations known to be fixed by means of genetic drift and not by selection. The drift probably operates at the same rate in frozen and plastic species. Still, 35 % of the substitutions (20-70 %, depending on the studied taxon) occur in short periods of speciation. By the way, this suggests that natural selection and genetic draft (evolutionary hitchhiking)⁽²⁹⁾, i.e. the two processes that operate most effectively in plastic species, play a far more important role in the accumulation of substitutions in DNA than is usually assumed by molecular taxonomists. It is worth mentioning that we are unaware of how many speciation events really occur in the studied seemingly unbranched lineages. Therefore, the published estimates of speciation-associated substitution rates only represent the lower margin of the real figures. Molecular studies also confirm increased rates of evolution in island species. These species not only have a higher substitution rate but also a higher frequency of nonsynonymous substitution among the observed mutations which suggests that positive selection rather than drift plays a more important role on islands (where higher frequency of peripatric speciation could be expected)⁽³⁰⁾.

Another corollary of the anagenesis-cladogenesis association predicted by the frozen plasticity theory is that the extant representatives of ancient phylogenetic tree branches that have sustained the lower number of speciation events should bear more plesiomorphic characters than the representatives of apical branches of the phylogenetic tree. According to classical theories of evolution no such correlation between species age and its antiquity should be expected.

The frozen plasticity theory also offers a new explanation for the existence of evolutionary trends, the slow directional phenotypic changes in organisms of particular phylogenetic lineages that endure much longer than the individual species involved. The main problem with the existence of such trends is that they are too slow to be geared by natural selection. The change in the value of the trait per generation is so small that it is absolutely invisible for natural selection⁽³¹⁾. According to classical evolutionary theories, the selection pressure has to be strong enough to overpower the effect of genetic drift. However, such selection should result in far more rapid evolutionary changes than that which come to light as evolutionary trends in the

paleontological record. The frozen plasticity theory suggests a new solution to the problem of very slow evolutionary trends. According to this theory, the trend could in fact be a product of a relatively strong and long-term selective pressure to which species can respond, however, only in short and rare periods of their evolutionary plasticity.

The probability of return from frozen to plastic state is rather low. Most attempts to colonize new areas which could potentially result in peripatric speciation probably end sooner or later with the extinction of the new population, fusion of the new population with the old one or with premature freezing of the newly plastic species due to gene flow from the mother population. It could be speculated that the abundance, population density and ecological valence of an old frozen species continuously decreases. This could result in disintegration of the population of an old species into a number of small subpopulations. It could be argued that such process could increase the probability of peripatric speciation and a consequent return to the plastic state in at least some of these geographic isolates. However, this scenario of cyclic rejuvenation of species seems to be rather improbable. The genetic impact of a random sampling of a gene pool of a species by colonization of a new area by a small number of individuals differs from that of a gradual reduction of a large population to a small number of individuals. In the former case, the proportions of different alleles in the sample (a colony) could radically differ from those in the original population in genetic equilibrium. In the latter case, the proportions of all alleles remain stable during the whole process of population reduction due to stabilization by frequency-dependent selection. Results from rigorous models are not available; however, in my opinion, the chance that genetic drift alone, without the help of the previous random sampling, might restore plasticity in a frozen species is rather low. Therefore, the destiny of most frozen species is probably extinction rather than plasticity restoration. Of course, a different situation could occur at the periods of mass extinction when a drastic environmental change brings many species to the edge of extinction. A renewed evolutionary plasticity of many species could in fact help rapidly restore the original biodiversity and even could even trigger the origin of evolutionary novelties and major evolutionary transitions in the ecosystem⁽³²⁾.

In a long-term perspective, the number of species on Earth is relatively stable or even grows⁽³³⁻³⁶⁾. If most species end their existence with extinction, then some species have to speciate many times. It is therefore highly probable that the species in a transiently plastic state usually splits off not one but several different species. It has already been pointed out by different authors that the shape of phylogenetic trees differ significantly from what is predicted by the neutral Darwinian model of random speciation and extinction^(31,37). The phylogenetic trees are usually shrub-shaped rather than tree-shaped. Most disparate species originate at the same time and

possibly from a common ancestor as a result of the process of adaptive radiation. Particular species, which have originated in a common radiation event and from a single evolutionarily plastic ancestor, coexist for a long time, without splitting off new species. Most branches end without producing a successor; however some of them could split off a new plastic species that could undergo a new burst of radiation. Interestingly, such a tree is similar in shape to the figure drawn by Charles Darwin⁽³⁸⁾ and unlike modern trees (which are usually automatically interpreted as phylogenetic trees but in fact inspired by the shape of the cladogram, a graphic representation of the distribution of synapomorphies within a studied taxon).

Other macroevolutionary phenomena that have no support in the classical evolutionary theories but can be explained within the frozen plasticity theory are decreased variability of species with age of the phylogenetic line and the maximum biodiversity, and disparity of a clade in particular, achieved rather early after the origin of the phylogenetic line (clade)^(39,40). Webster⁽⁴¹⁾ has reported that the frequency and extent of morphological variation in 982 trilobite species are greatest early in the evolution of the group. He has shown that “the proportion of species with at least one polymorphism drops sharply between the Middle Cambrian (75%) and Late Cambrian (8%), then rises to 40% in the Early Ordovician (coincident with the first sampling of the diverse phacopid and proetid orders), after which there is a progressive decline through the Middle Devonian (1%), interrupted only by a particularly low value (0%) in the Late Silurian. No polymorphism was recorded in character-state coding among the 23 post-Devonian species. Genera originating in the Cambrian had shorter average durations than genera originating in the post-Cambrian⁽⁴²⁾, resulting in accrual of lower species-level diversity per genus.”

The graphs of change in the diversity of a clade are usually asymmetrical in time; it takes a relatively short time for a clade to achieve the maximum diversity and a long time to go extinct^(40,43). It was also shown that the speciation rate usually declines with the age of a clade^(44,45). Both phenomena (higher variability of early-branched species and decreasing speciation rate of clades) could have a common cause, namely the continuous irreversible freezing of more and more traits during the evolution of a clade. It is sure that the traits differ in resistance to transition from frozen to plastic in response to reduction of genetic polymorphism. This process is likely to happen readily for some traits and can be achieved by a relatively small reduction in genetic polymorphism. For other traits, the transition from frozen to plastic is difficult or even impossible, as it needs an unrealistically small founding population and an unrealistically long period of persistence of such a small population in an extinction-prone state. On a macroevolutionary time scale, more and more traits pass into the permanently frozen state due to a universal process of sorting on the basis of stability⁽³¹⁾. The stable traits (and systems and

anything) persist while the unstable traits (and systems and anything) pass away. An example of a stable trait is a trait that is coded by many genes that are substitutable in their effect. The mutation of an allele in one locus (or several loci) does not result in the change of such a trait. At the same time, the mutation in all loci is highly improbable especially if, due to pleiotropy, the genes in particular loci also influence other traits. Another source of the evolutionary stability of a trait is frequency-dependent selection, particularly the steep dependence of fitness on the frequency of a particular allele. When the fitness of an individual sharply decreases with an increased frequency of an allele (of a particular trait, strategy), even a drastic reduction in population size cannot lead to total loss of polymorphism in a particular locus and corresponding trait. Due to dominance and especially due to epistatic interactions of more than two genes, the slope of the fitness function can be very steep. In the former case, the fitness of homozygotes with genotype aa could decrease at a rate proportional to the second power of the trait frequency. In the latter case, the rate could even be proportional to a higher power of the trait frequency. This kind of trait probably survives peripatric speciation in a polymorphic state, or polymorphism in such a trait is restored very quickly in the originating new species due to mutations.

In a new clade, a high proportion of species contain many traits that could melt during standard peripatric speciation or that are relatively plastic even on the level of a species (or even of a local population). Through time, more and more traits in more and more species turn to a semipermanently or even permanently frozen state. The representatives of a particular clade are not only less and less variable (more and more elastic – resistant to selection pressure) but also exhibit elasticity that is less and less affected by peripatric speciation. Originally, many representatives of a clade had the capacity to evolve new body plans after peripatric speciation. In the end, only some species retain this capacity and even in these species some traits had a highly limited capacity to respond to selection after peripatric speciation.

In fact this mechanism can explain another well-known phenomenon, namely: dead clade walking. It is widely known that unexpectedly many diversified and diversifying clades that survive a period of mass extinction, turn marginal or decline in the aftermath stage. Jablonski⁽⁴⁶⁾ wrote that “For four of the Big Five mass extinctions of the Phanerozoic, the marine genera that survived the extinction suffered about 10–20% attrition in the immediately following geologic stage that was significantly greater than the losses sustained in preextinction stages. The stages immediately following the three Palaeozoic mass extinctions also account for 17% of all order-level losses in marine invertebrates over that interval, which is, again, significantly greater than that seen for the other stratigraphic stages (no orders are lost immediately after the end-Triassic or end-Cretaceous mass extinctions).” Such pattern could be expected when representatives of a

particular clade that survived the mass extinction were irreversibly frozen. A clade depleted of all species that can be turned to the plastic state by peripatric speciation, cannot adapt to the changing environment and would highly probably turn extinct in the next chronostratigraphic stage.

Another phenomenon that cannot be explained within traditional evolutionary theories is the Cambrian explosion – the rapid origination of probably all extant (and also many other already extinct) metazoan phyla around 545 millions years ago^(47,48). All of the basic architectures of animals were apparently established by the close of the Cambrian explosion; subsequent evolutionary changes, even those that allowed animals to move out of the sea onto land, involved only modifications of those basic body plans. Most probably, not only the general diversity of metazoan body plans, but also the diversity within particular phyla reached its maximum within 10-15 million years of the Cambrian, and decreased throughout the following 500 million years^(47,49). The number of species increased irregularly and discontinuously during the Phanerozoic; however, the number of body plans, i.e. disparity, decreased. There was a large effort to “unexplain” the Cambrian explosion⁽⁵⁰⁻⁵³⁾, a phenomenon that had no support in contemporaneous evolutionary theories^(54,55). Molecular clock data based on concatenated amino acid sequences of 129 proteins from 36 eukaryotes suggests that representatives of metazoan phyla probably diverged 100-210 million years before the Cambrium⁽⁵⁶⁾. (The previous molecular studies suggested an even earlier divergence time, however, the result of current multigene studies are more reliable). Nevertheless, this data is useful for tracking events of cladogenesis, but not events of anagenesis⁽⁵⁷⁾. The metazoan phyla could diverge long before the Cambrian, most probably, however, their representatives had very similar body plans until the beginning of the Cambrian when some extrinsic (ecological) or intrinsic (genetic) event probably triggered the morphological diversification of the metazoa.

The existence of the Cambrian explosion is in accord with the predictions of the frozen plasticity theory. In the beginning of the evolution of the metazoan clade, many traits, even those that determine the basic architecture of animal body plans, had the capacity to turn plastic during peripatric speciations in many metazoan lineages. Therefore, a rather radical remodeling of body architecture as well as the origin of new body plans in response to particular selection pressures, were possible in the early stages of metazoan evolution. Through time, more and more traits had come to be permanently frozen. Most probably, different traits would lose the capacity to turn plastic in differing successions in particular phyla. Therefore, anagenetic potential faded and adaptation to the new environmental conditions came to be based on modification of existent body plans rather than on building new ones. We can perform the following thought experiment: Imagine that something, e.g. a virus or humankind, kill all metazoan species on Earth with the

exception of a single cockroach species. According to classical evolutionary theories, given enough time, the survivor cockroach species would differentiate into many new phyla with radically different body plans to exploit (and to build) all available niches. According to the frozen plasticity theory, the survivor cockroach species would more probably differentiate into many new species of cockroaches while most niches on Earth would probably remain empty (and unestablished).

The theory of frozen plasticity suggests that the taxonomic category of species, and possibly even that of genus, could objectively denote the existing entity, rather than a merely useful epistemological construct of biologists. Within the theory of frozen plasticity, a biological species can be defined as a set of individuals sharing an identical gene pool throughout the period between two speciating events. Similarly, a genus can be defined as a set of individuals sharing a common exclusive ancestor in the period between two periods of evolutionary plasticity.

Conclusions

The main purpose of the present article is to show that the new picture of evolution postulated by the frozen plasticity theory differs in many respects from what is assumed by classical evolutionary theories and presented in all textbooks of evolutionary biology. The existence of the plastic and frozen phases in the life of a species resulting in a punctuated equilibrium pattern of evolution^(58,59) is now a widely accepted model of the evolution of multicellular life on Earth. The frozen plasticity theory suggests that certain rather probable hypothesis on the nature of evolutionary stasis (frequency-dependent selection and pleiotropy-based elasticity of genetically polymorphic species) and evolutionary plasticity (loss of genetic polymorphism due to the founder effect during peripatric speciation, and drift following it) could have a very important impact, not only on macroevolutionary but also microevolutionary and ecological processes (Table 1). In fact, the picture of evolutionary and ecological processes presented by the frozen plasticity theory differs in many respects from that provided by the current textbook theory of evolution. Most of these predictions could be tested empirically and should be analyzed in greater depth theoretically. In my (very subjective) opinion, the frozen plasticity theory, which includes the Darwinian model of evolution as a special case – the evolution of species in a plastic state, not only offers plenty of new predictions to be tested, but also provides explanations for a much broader spectrum of known biological phenomena than classic evolutionary theories.

Acknowledgements

The author thanks especially P. Baum, F. Cvrčková, D. Frynta, S. Komarek, A. Markoš, D. S. and J. Zrzavý for their suggestions and inspiring discussion. This work was supported by grant No. 0021620828 of the Czech Ministry of Education, Youth and Sports.

Table 1. Differences between predictions of the classical theories of evolution and frozen plasticity theory of evolution. Two asterisks denote the predictions that have already been tested and support the frozen plasticity model. One asterisk denotes the predictions that have not been intentionally tested but are supported by published data. ^{1(70), 2(28), 3(60,61), 4(62), 5(3), 6(6), 7(63), 8(23,24), 9(22), 10(16-18), 11(7,8)}.

	classical theory	frozen plasticity theory
anagenesis and cladogenesis ^{**1, 2}	are independent	are coupled
divergence of species ¹	does not correlate with taxon richness	correlates with taxon richness
genetic polymorphism ^{**3}	accelerates evolution	decelerates evolution
species respond to selection ^{*4}	plastically (as plasticine)	elastically (as rubber)
species are adapted to ^{*5}	current environment	original environment
local and global abundance ^{**6}	correlate for any species	do not correlate for old species
abundance of species	is independent of species age	decreases with species age
ability of species to respond to environmental changes ^{**7}	is independent of species age	decreases with species age
species on islands are derived ^{*1}	as much as those on continents	more than those on continents
asexual species ^{*8}	less adapted to their environment	more adapted to their environment
cross-pollinating species ^{*9}	as stable as self-pollinating species	more stable than self-pollinating species
invasive species ^{**10}	express average heritability	express higher heritability
domesticated species	express average heritability	express higher heritability
domesticated species	express average age	are evolutionarily younger
successful selection ^{*11}	has no influence on fitness	decreases fitness
rate of anagenesis in a clade [*]	is (on average) constant	usually decreases
two species in the same niche [*]	usually cannot coexist	frequently can coexist
slow long-term trends [*]	are hardly possible	are quite possible

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