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Dynamic evolution hypothesis of organisms

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Abstract: I propose a dynamic evolution hypothesis regarding the evolution of organisms by incorporating both diminished fitness returns and mutation rate tuning during adaptation to a constant environment. Basically, accumulating evidence from life history studies conducted over the past 70 years suggests that the evolution of individual fitness is subject to ecological constraints, leading to the evolutionary existence of an upper limit of individual fitness (ULIF). Given the existence of the ULIF, organismal evolution, which might initially have relatively great fitness returns through primarily Darwinian evolution, will eventually be subject to diminished fitness returns towards zero. With the diminished fitness return, Darwinian selection strength may eventually become smaller than the power of random genetic drift, leading to the occurrence of neutral evolution at both phenotypic and molecular levels. Meanwhile, mutation rates may change from an initial increase, due to the relatively strong fitness return, to subsequent decreases, due to both the diminished fitness return of beneficial mutations and the cost of deleterious mutations. The diminished fitness returns with subsequently reduced mutation rates are two potential evolution barriers leading to eventual evolutionary stasis. These findings provide important insights for understanding the conditions for the occurrences of different evolutionary patterns. Darwinian evolution theory, neutral evolution theory and punctuated equilibrium theory can be unified in the context of the dynamic evolution hypothesis formulated in this study.

Keywords: Diminished fitness return, mutation rate tuning, Darwinian evolution; neutral evolution; punctuated equilibrium; unified evolutionary theory

Introduction

Since Darwin's proposal of the theory of natural selection (*1*), many alternative evolutionary theories have been proposed. These evolutionary theories generally validate the role of natural selection in causing adaptive evolution but contribute new knowledge regarding evolutionary patterns. For instance, the punctuated equilibrium theory indicates that although there are evolutionary lineages displaying phylogenetic gradualism, as Darwin predicts (*2*), many or even most evolutionary lineages display an initially rapid evolution and then a subsequent long-term evolutionary stasis, often for millions of years (*3*). Similarly, the neutral theory of molecular evolution asserts that although some evolutionary changes at the molecular level are caused by natural selection, a vast majority of molecular substitutions are fixed by random genetic drift and are therefore subject to neutral evolution (*4*). With respect to these evolutionary theories, the present evidence demonstrates that all known diverse evolutionary patterns, including phylogenetic gradualism, punctuated equilibrium (evolutionary stasis), selective evolution and neutral evolution, largely occur in real life (*5-17*), suggesting the mosaic evolution of organisms in terms of evolutionary patterns. Given the mosaic evolutionary patterns, to date, there is no known single evolutionary theory that is able to consistently take all of these patterns into account simultaneously, unless it is assumed that organismal evolution is a dynamic process and that these diverse evolutionary patterns may merely be its variable results.

The current evidence from the fields of paleobiology, ecology, molecular evolution and experimental evolution consistently points to the possible dynamic evolution of organisms' characteristics, though not necessarily in the forms of shifting between different evolutionary patterns, as mentioned above. For instance, fossil records document that many species' evolutionary histories are characterized by a rapid speciation and then a subsequent prolonged evolutionary stasis (*3, 5*). Comparative molecular evolutionary studies reveal widespread evolution rate variations among genes (*18, 19*). In addition, comparative phylogenetic analyses of phototransduction genes show that apparently positive Darwinian selections are largely restricted to very few branches associated with diel activity shifts, rather than occurring extensively across phylogenetic branches (*20-22*), suggesting the pulsed adaptive evolution of organisms. Ecological studies show that increased investments into reproduction and lifespan may not always lead to increases of individual fitness, but their contributions to individual fitness will eventually decrease to virtually zero due to ecological constraints, leading to selection against further investments (*23-26*). In particular, long-term studies on experimental evolution demonstrate that organismal evolution is subject to decreased fitness returns with increased adaptations in constant environments (*27-40*); meanwhile, mutation rates also exhibit adaptive tuning with an initial increase and subsequent decrease as the putative adaptation peak is achieved (*31, 35, 39-50*). Moreover, one laboratory-based evolutionary study demonstrates a transition from selective evolution to neutral evolution with increased adaptation (*34*). All of these findings across different fields provide evidence for the possible dynamic evolution of organisms.

Given the ubiquitous dynamic evolution of organisms, seeking one general mechanism underlying dynamic evolution seems to be of particular significance for understanding the occurrence of mosaic evolutionary patterns in organisms. In this study, I will begin with the evolutionary ecological analyses of individual fitness evolution under ecological constraints based on empirical studies. On the basis of the ecological constraints on individual fitness evolution, I will demonstrate a dynamic evolution mechanism incorporating environmental dynamics, selection intensity changes and mutation rate tuning during adaptation, which inspires the formulation of a dynamic evolution hypothesis for organismal evolution. The dynamic evolution hypothesis can predict the occurrences of different evolutionary patterns and provide important knowledge to the field of unifying different evolutionary theories.

Ecological constraints and the upper limit of individual fitness evolution

Darwin's theory of evolution predicts that natural selection will maximize individual fitness. Ideally, maximum individual fitness occurs if one parental individual itself leaves an infinite number of offspring per unit time through, for instance, a continuous increase of clutch size and lifespan, which is the so-called Darwinian Demon (*51*). However, for the past 3.5 billion years since the origin of life, a vast number of life forms have evolved with numerous lifestyles, but no instances of the Darwinian Demon have been observed, and no one is known to have achieved such maximum individual fitness (*52*). In contrast, almost all organismal individuals only produce a certain number of offspring in their lifetimes. For instance, a female elephant normally only has one calf at a time and, on average, will give birth to seven offspring in her lifetime. This finding may suggest the evolutions of individual fitness are generally constrained, assuming the correctness of Darwin's natural selection theory.

To date, there is not considerable knowledge regarding the crucial constraint factors that underlie the evolution of individual fitness. Simply stated, fitness is a result of the interaction between organisms and environments. Organisms themselves can evolve in order to promote their fecundity and survival, despite possible genetic constraints (*53, 54*), but their evolutionary survival ultimately depends on certain environmental resources (e.g., food, water, shelter and space). It is well-known that environmental resources are generally limited relative to rapidly increasing populations (*1, 55, 56*), which leads to an inevitable limitation on per capita consumption of resources due to competition among individuals of the same species. The limitations of per capita resource availability may be an important constraint on individual fitness evolution. For example, avian clutch sizes are believed to be largely constrained by food availability that one parental individual is able to access during the breeding seasons (*23, 24*). Given the limitations on resources, if organisms (e.g., vagrants) shift to exploit additional resources, for instance, to use other species' specific resources, or to access potential resources across their range boundaries, this may then incur substantial fitness costs due to unfavorable abiotic conditions (e.g., extreme low temperature) and/or antagonistic biotic interactions (e.g., competition and predation) (*57-63*). The increased fitness costs may be a crucial factor for selecting against vagrants to lead to their niche conservatisms (*61, 62, 64, 65*), which will, in turn, inevitably constrain the increase of individual fitness.

In addition to the constraints in acquiring additional resources, there are other possible negative ecological factors that may also constrain the evolution of individual fitness. One such factor is predation. For instance, it is considered that larger avian broods may be noisier and require more frequent feeding and may hence be more likely to be spotted by predators, leading to high predation risks for both parents and offspring (*66-70*). Moreover, some density-dependent mortality factors, such as competition, disease and parasitism, cannot be neglected, as increased clutch sizes may lead to the high mortality rate of offspring through relatively intense competition and prevalence of diseases and parasitism among offspring (*26, 67, 71-73*). The negative correlation between increased reproduction efforts and the survival of both parents and/or offspring suggests the trade-off between reproduction and survival, which may be a potentially important constraint on individual fitness evolution in each reproductive brood (*26, 67*). In addition to these constraints, certain constraints exist that limit the maximum number of clutches that can be raised in the lifetime of one parental individual. For instance, the breeding periods of most organisms are primarily restricted to a specific period in the year when climates and food conditions are favorable for the rearing of offspring (*67*). Moreover, the occurrence of senescence is another crucial constraining factor. The classic evolutionary theory of senescence suggests that the organismal lifespan cannot be infinitely extended because the forces of natural selection decline with age, since all organisms eventually inevitably die of extrinsic factors, such as diseases, accidents, and predation (*25, 26*). This finding may suggest that lifespan and hence lifetime reproduction times are generally constrained by external ecological factors, as well.

Taken together, individual fitness evolution is clearly constrained by many potential ecological factors (*23-25, 61, 74, 75*) (Fig. 1). In addition to these ecological factors, other factors, such as evolutionary constraints (*53, 54*), mechanical constraints (*76*), and biochemical and physical constraints (*29*), might also have variable negative effects on the evolution of individual fitness. And all of these constraints, especially those extrinsic factors, may negatively affect the evolution of individual fitness. It is apparent that these constraints may become even stronger with increased individual fitness, leading to the bottleneck of individual fitness evolution because, for example, an increased individual fitness may require organisms to acquire additional resources and face increasingly unfavorable ecological conditions, which will incur substantial fitness costs (*57-65*). Therefore, it is more likely that the lifetime offspring number of each parental individual cannot be increased to an infinite extent, but there might be a general existence of an upper limit of individual fitness (ULIF) for most, if not all, life forms. Given the ULIF, to date, we do not know exactly what the value might be, while it may vary among species due to their specific constraints. We may expect that future theoretical life history studies may help to determine the ULIF for each species.

Diminished fitness returns with adaptation

Organisms evolve to promote their fitness, but their increased fitness is accompanied by a series of increased constraints, which may eventually result in the existence of a ULIF for each taxon, as described above (Fig. 1). Considering organisms initially adapting to a newly constant environment, for their reproduction-related traits (e.g., clutch size), their beneficial mutations may gain certain fitness returns and individual fitness may grow continuously. However, with the continuous increase of individual fitness, population size may also grow, and the residual space left for the further increase of individual fitness must become increasingly smaller due to the increasing ecological constraints (e.g., competition, predation and limitations of resources) on the evolution of reproduction-related traits, eventually leading to their decreased fitness returns. Unlike reproduction-related traits (e.g., clutch size), which evolve to directly increase the number of offspring, for survival-related traits, their evolutions are dedicated to promoting an organism's survival, and apparently, their contributions to fitness have an upper limit value as an organism's survival rate climbs to 100 percent. Given the existence of the upper limit of fitness contributions of survival-related traits which, however, is not the result of ecological constraints, it must suggest that the evolution of survival-related traits are also subject to diminished fitness returns as offspring survival increased to a certain extent. For instance, in regards to cold tolerance, its contribution to fitness must decline as organisms' adaptation to cold is achieved to some extent such that no individuals will die of extremely low-temperature once again. Actually, given the existence of ULIFs, the evolution of both reproduction-related traits and survival-related traits may eventually follow the "Law of Diminishing Returns", a universal principle in economics (*77*). An extreme case is that the further evolution of any traits, even including those that are the most potentially favorable beneficial variations, may gain no fitness response as organisms have evolved to achieve a certain ULIF resulting from ecological constraints, despite their possible infinite evolutionary potential. The occurrence of fitness return reduction may be not due to the beneficial mutations themselves but may be observed because their fitness effects cannot perform sufficiently under the circumstances, such as suffering from the bottleneck effect of individual fitness evolution that is the result of extrinsic constraints.

Ecological and laboratory studies have provided strong support for the existence of the diminished fitness return with increased adaptations. For instance, ecological studies show that an increased avian clutch size will eventually lead to a decreased fitness return due to the limitations of resources and/or negative ecological interactions (*23, 24, 26, 66, 68*). Similarly, it is suggested that an increased investment in extending organismal lifespans may be less effective because selection strength declines with age according to the evolutionary theory of senescence (*25, 26*). In terms of laboratory studies, previous studies on enzyme activity have demonstrated that increased enzyme activity will eventually result in diminishing returns in fitness due to substrate availability (*78, 79*). Moreover, the diminished return in fitness with the increase of adaptation is also a recurrent pattern observed in experimental evolution research (*27-40*). The diminished return of fitness observed in experimental evolutionary studies to date has been mainly explained as a result of clone inference and/or diminishing returns epistasis (*27-30, 33, 37, 40*). However, it is more likely that with the increase of adaptations to new experimental conditions, the ecological constraints, such as the limitations of per capita consumption of resources (e.g., nutrients and space) due to individual competition within laboratory populations, could contribute to the reduced fitness return, as well. Actually, the so-called diminishing returns epistasis is likely only the proximate explanation of the observed reduced fitness return. And the ultimate cause of the observed reduced fitness return may be partly attributed to extrinsic factors, such as the ecological constraints emphasized in this study and, if any, other possible biochemical and physical constraints (*29*).

Though there is a ULIF, whether organisms will eventually reach it remains uncertain. The uncertainty occurs because random genetic drift must eventually delay the increase of individual fitness with the decrease of marginal fitness returns of beneficial mutations (Fig. 1). In particular, when the decrease of marginal fitness returns of beneficial mutations reach a critical point, where its selection coefficient is lower than the power of random genetic drift ($s < 1/2N_e$), the fixation of the beneficial mutation is more likely dominated by drift, leading to its neutral evolution (*4, 9-12, 78, 80*). It is conceivable that the effects of drift will become increasingly large with gradually decreased marginal fitness return of those potential beneficial mutations, as evidenced by an experimental evolution study (*34*). An extreme case is that all of the potential beneficial mutations may be subject to purely neutral evolution as their marginal fitness returns are expected to reach to zero if the ULIF is achieved. It is noteworthy that despite the strong interference of drift at later times, beneficial mutations may be still favored by directional selection due to even its minor advantages, and we may expect that the evolution of individual fitness may infinitely approach the ULIF but possibly never reach it due to extremely weak Darwinian selection relative to the strong interference of random drift upon entering the period of fitness bottleneck (Fig. 1).

Rise and fall of mutation rate

Provided that organismal evolution is subject to diminished fitness returns, the mutation rate of organisms may be subject to adaptive tuning, as well. Considering the organisms invaded into a newly constant environment, the organisms may evolve to reach to a certain ULIF under direction selection. Directional selection, which always favors extreme phenotypes, may lead to an increased mutation rate as a result of the hitchhiking of mutators with beneficial mutations (*31, 39, 40, 42, 43, 47, 49, 50, 81-83*). An increased mutation rate, to a certain extent, may accelerate the rise of beneficial variations and promote individual fitness (*31, 39, 40, 42, 43, 47, 49, 50, 81-83*). For convenience, I refer here to directional selection for increased genetic variation as a heterogenizing selection. Under heterogenizing selection, mutation rates may increase continuously. However, considering that most mutations are deleterious, mutation rates may not increase infinitely. When mutation rates increase to the point where their marginal fitness returns are equal to their marginal fitness costs, mutation rates will reach their maximum values and cease to increase.

Maintaining a maximum mutation rate might always be favored by heterogenizing selection if all else remains unchanged. However, as described above, there is a ULIF, and the marginal fitness return of beneficial mutations will eventually be reduced. Consequently, we then may expect mutation rates to start to decrease as their marginal fitness returns become lower than their marginal fitness costs. An extreme case is that when a certain ULIF is achieved, mutation will convey no advantage but only has net negative effects, and then selection must begin favoring a relatively low mutation rate. To distinguish from the heterogenizing selection referred above, I hereby refer to directional selection of a reduced genetic variation as homogenizing selection. Unlike heterogenizing selection, homogenizing selection will essentially reduce the mutation rate, leading to an increased genetic identity between parent and offspring. Ideally, under homogenizing selection, mutation rates may be expected to approach zero. Though due to this, the decrease of mutation rates may eventually be constrained by several potential factors, such as the cost of fidelity, intrinsic physiological limitations and random genetic drift (*46, 47, 84, 85*). Particularly, random genetic drift is considered to become a predominant force for countering the decrease of mutation rate because, as mutation rate decreases to an extremely low value by selection, the fitness conveyed by the decrease of mutation rate will eventually become negligible, and then selection will be incapable of reducing the rate any further due to the interference of random genetic drift (*86-89*).

To date, the adaptive tuning of mutation rates has been documented using laboratory evolution experiments of microorganisms adapting to new conditions (*31, 35, 39-50*). For instance, one long-term experimental evolution on *Escherichia coli* adapting to a new medium shows its mutation rate is increased by approximately 150-fold, and then reduced up to 60 % by increased adaptation (*39*). For sexual organisms, their increased mutation rates as they adapt to new environments are also suggested by simulation studies, despite the possible negative effects of recombination (*90-92*). Given the adaptive tunings of mutation rates, almost all previous studies assume that under new selection pressures, organisms may be selected to increase their mutation rates to produce beneficial mutations quickly and speed up adaptation (*31, 39, 40, 42, 43, 47, 49, 50, 81-83*); however, as previously mentioned, once organisms become well-adapted or achieve their adaptive peak or optimum, their mutation rates will then become subject to decrease due to the high detrimental effects of deleterious mutations (*31, 39-43, 45, 47-50, 82, 93*). In this regard, I agree that the cost of deleterious mutations is no doubt an important contributor causing the decrease in mutation rate, but their implicit assumption of achieving an adaptive optimum or well-adaptiveness may be not accurate. Actually, the adaptive optimum, although theoretically valid, is probably never reached. However, it would be more plausible to alternatively explain the decrease of mutation rate as the combined effects of both diminished fitness returns of beneficial mutations with increased adaptations and deleterious mutation costs.

Evolution barriers and evolutionary stasis

The findings mentioned above suggest that organisms' evolution will be subjected to a diminished fitness return towards zero with increased adaptation, and eventually, all beneficial mutations of an organism's traits may gain minor or no marginal fitness returns, leading to their neutral evolution. Meanwhile, with the reduced fitness return of organisms' evolution, mutation rates may be reduced to an extremely low value, which may then reduce raw materials for further evolution. The diminished fitness returns with subsequently reduced mutation rates can be considered to be a linkage mechanism to constrain further selective evolution and neutral evolution and can be referred to as two evolution barriers. Under the dual evolution barriers, organisms may still evolve to approach their ULIF due to the existence of minimum mutation rates at later times but essentially show little evolutionary change such that it may be regarded as evolutionary stasis. The status of evolutionary stasis may remain unchanged, given that the environment remains permanently stable and no new selection further occurs. Of course, taxa being at the stages of evolutionary stasis may be particularly prone to extinction due to their extremely reduced mutation rates and hence weak evolution potential. Given the existence of evolution barriers, we may expect that organismal traits may be far from absolute perfection (e.g., Darwinian Demons), a claim discussed in different contexts by others as well (*78, 79, 94, 95*), but rather, they may be merely a transient evolutionary consequence partly resulting from extrinsic constraints.

Evolutionary stasis is a common phenomenon in the fossil record and is invoked as the claim of punctuated equilibrium theory (*3, 6-8, 16, 17*). To date, evolutionary stasis has been considered to be a result of many potential causes, including but not limited to stabilizing selection (*96, 97*), genetic and developmental constraints (*3, 7*), cohesion of genotype (*98*), homogenizing effects of gene flow (*54, 99*) and geographic structure (*5*). Among these causes, stabilizing selection and genetic constraints are two of the most commonly invoked explanations (*100*). Disentangling these explanations is beyond the scope of this study, and in fact, many of them have been criticized elsewhere, including stabilizing selection, genetic constraints and gene flow (*3, 5-7, 54, 96-98*). However, it seems that one major problem for these explanations, if not all of them, is that they cannot explain why many species have been capable of evolving continuously without entering stasis. Nonetheless, the evolution barriers stemming from the diminished fitness returns and reduced mutation rates recognized in this study does offer an alternative explanation for the occurrence of evolutionary stasis. Accordingly, it could predict that those species must eventually fall into evolutionary stasis if their environments remain stable and no new selection further occurs, whereas for those species that are subject to continuous new selections, they should be subjected to continuous evolutionary changes instead of evolutionary stasis, assuming no extinction occurs. The evolution barriers recognized in this study may be an important factor for causing stasis.

Regarding the role of stabilizing selection in causing stasis, though valid in theory, it seems to be a meaningless concept at this juncture because it rests on the assumption of the existence of the adaptive optimum of phenotypes (*76, 96*), but organisms would never reach to or even be far from that theoretically absolute optimum value (*78, 79, 94, 95*), particularly considering the existence of evolution barriers as recognized in this study. Specifically, to adapt to a new environment, the average value of organismal phenotypes will evolve continuously to approach a certain ULIF under directional selection and will eventually reach a relatively static evolutionary state (evolutionary stasis) close to, but never beyond the ULIF, due to evolution barriers. The relatively static evolutionary state of phenotypic evolution apparently by no means represents achieving an adaptive optimum resulting from so-called stabilizing selection, but it is rather merely a transient evolutionary consequence. Therefore, it is probably given that in natural populations the adaptive optimum-based stabilizing selection may be untenable (*101*) even in stable environments, while directional selection may dominate evolution in organisms, no matter how negligible its strength may eventually become as phenotypes approach the ULIF. If this is true, it should substantially challenge the traditional Darwin school's explanation about evolutionary stasis based on the rationale for adaptive optima under stabilizing selections (*96, 97*), which has also been questioned by many authors in different contexts (*6, 7, 54, 98, 102*).

Selection dynamics and the unification of evolution theories

This study shows that both selection intensity and mutation rate will be subject to dynamic changes partly due to diminished fitness returns with increased adaptation. In the initial stages of adaptation to a new environment, the fitness return of a beneficial mutation is relatively great, and the mutation rate may increase under heterogenizing selection. This increase will lead to an accelerated evolution, mainly in the Darwinian manner. However, at later times, with the diminished fitness return, both selection intensity and mutation rate will be reduced. This phenomenon will then lead to a decreased evolution rate and even evolutionary stasis. The dynamic process of adaptive evolution from an initially accelerated evolution to an eventually evolutionary stasis, which strikingly resembles the pattern of punctuated equilibrium, may be regarded as an adaption cycle. Evolutionary stasis, of course, may be broken as new selections occur. And at that time, the ULIF may be reset and the population will enter another cycle of adaptation. Regarding punctuated equilibrium patterns, the traditional explanation for the observed accelerated evolution during speciation rests on possible genetic revolution putatively occurring in small and isolated peripheral populations (*3, 98*). However, the initially great fitness return of beneficial mutations and increased mutation rate demonstrated in this study provide an alternative explanation, and it is suggested that an initially accelerated evolution of organisms may be an inevitable result as they adapt to new selection pressures. If this is the case, it may suggest punctuated equilibrium patterns may widely occur as adapting to new and stable selections; hence, its occurrences may not just be necessarily restricted to those specifically isolated peripheral populations originally invoked by punctuated equilibrium theory (*3*).

This study also demonstrates the possible occurrence of neutral evolution (Fig. 1), in addition to the occurrences of evolutionary patterns of Darwinian evolution and punctuated equilibrium. In adapting to a new and stable environment, it has been shown that both selection intensities and mutation rates in populations may decline with the diminished fitness returns of beneficial mutations, and correspondingly, potential beneficial mutations will shift from their initially predominant Darwinian evolution to an eventual neutral evolution as their selection power becomes lower than that of random genetic drift (*4, 9*-*12*). In addition, particularly, the neutral evolution may become a predominant force if the marginal fitness returns of beneficial mutations are reduced to extremely low values, as Darwinian evolution becomes almost negligible at that time (*4, 9*-*12*). Thus, the diminished fitness returns may be regarded as another potential extrinsic source to contribute to neutral evolution, besides for previous well-known neutral substitution sources, such as the mutations occurring in synonymous sites, silent sites (introns) and pseudogenes, and those possible functionally equivalent mutations facilitating adaptation (*4, 9*-*15*). It should be noted that traditional neutral theory almost exclusively emphasizes the possibility of neutral evolution at the molecular level (*4, 10, 13*), but this study suggests that neutral evolution may also be prevalent at the phenotypic level as entering a period of fitness bottleneck, since diminished fitness returns should be capable of applying to both molecular and phenotypic levels.

The dynamic evolution process characterized by the adaptation to a constant environment mentioned above sheds light on the conditions needed for the occurrence of differently known evolutionary patterns. To date, phylogenetic gradualism, punctuated equilibrium (rapid speciation with subsequent prolonged evolutionary stasis) and neutral evolution are regarded as three main evolutionary patterns.

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The findings of this study indicate that if the selection pressures of a new environment are fixed and remain unchanged, organisms will necessarily undergo an initially accelerated evolution and eventually enter a neutral evolution zone and fall into evolutionary stasis (Fig. 1), assuming no extinction occurs. This finding may suggest that the initially accelerated evolution of organisms may be an inevitable result of adapting to new selection pressures, and evolutionary stasis and neutral evolution may primarily occur by entering the periods of fitness evolution bottlenecks if no new selection pressures further occur. Unlike evolutionary stasis and neutral evolution, the occurrence of continuous evolutionary changes, and hence phylogenetic gradualism, may require continuously novel selection pressures, as evidenced by artificial selection experiments and the evolution of drug resistances in microbiomes. Otherwise, if organisms experience new selection pressures only once, for example, invading into a new and constant environment, they will evolve in the form of punctuated equilibrium instead of constant phylogenetic gradualism. It is therefore believed that organisms’ evolution may be largely considered to be a dynamic process, in which the occurrences of different evolutionary patterns seem to be largely determined by their selection dynamics.

Organismal evolution in real environments

In real environments, different organisms may have been confronted by variable survival conditions and hence may suffer from different selection dynamics. Continuously changed selections may occur as organisms’ environments suffer continuous changes on a time scale (e.g., global warming or coevolution interaction), while constant selection pressures may occur as the environments of organisms remain stable. The two typical environmental models may occur both in real life as Earth’s environments change across space and time but meanwhile remain relatively stable in other certain time or space scales. This phenomenon is particularly notable for abiotic environments. For instance, once deserts, oceans and highlands formed, they could experience fewer changes for up to several millions of years. Unlike abiotic environments, biotic environments seem to be less stable due to possible coevolution between interacting species. Coevolution may lead to continuous evolutionary changes between interacting species (*103*). However, coevolution seems to not occur universally, and in fact, clear evidence of coevolution is still scarce (*104-106*). It has been suggested that in real environments, a species is usually embedded in a multi-level interaction network, and this will lead to a definite low chance for strict one-to- one coevolution to occur (*105*). Moreover, the prevalence of living fossils and evolutionary stasis of species in the fossil record (*16*) may further suggest that noticeable coevolution changes at the species level may not occur widely, but may only be restricted to specific groups. Therefore, similar to abiotic environments, biotic environment may also be relatively stable for many species.

Therefore, in the natural world, some organisms may be confronted with continuous environmental changes, while others may have a relatively stable environment. The variable environmental conditions may exert different selection dynamics, leading to their diversified evolutionary patterns (*76, 107*). Phylogenetic gradualism is more likely to occur in continuously changing environments, while evolutionary stasis and neutral evolution may mainly occur in environments that remain stable over the long-term, which could also be achieved through habitat tracking (*5, 108, 109*). Regarding the evolutionary stasis and neutral evolution, which may mainly occur in stable environments, it should be noted that their occurrences may also be possible in some phenotypes or genes as environmental changes occur. This finding is observed because environmental changes are often restricted to the changes of limited environmental factors, rather than whole factors, and correspondingly, organismal adaptive evolution may mainly occur only in those specific phenotypes or genes responding to the environmental factor-specific selections, rather than at entire species level, whereas for those phenotypes or genes that their corresponding selection factors remain unchanged, they may still retain their previous evolutionary statuses, e.g., evolutionary stasis and neutral evolution. This phenomenon may lead to the variation of evolution rates and mosaic evolution at both phenotypic and molecular levels, a common pattern observed in morphological and molecular evolution studies (*18, 19, 76, 110*). These possibly loose conditions of the occurrences of evolutionary stasis and neutral evolution in both stable environments and changing environments, at least at the levels of phenotypes and molecules, may help to explain why evolutionary stasis is common (*5*) and why most molecular substitutions are selectively neutral (*4, 9-12*).

Conclusions

This study demonstrates that the occurrences of different evolutionary patterns are rooted in environmental dynamics. In continuously changing environments, organisms may evolve in the form of phylogenetic gradualism, but in stable environments, organisms must eventually enter a neutral evolution zone and fall into evolutionary stasis, assuming no extinction. Basically, empirical evidence suggests that there is generally an evolutionary existence of the ULIF due to ecological constraints. Given the existence of the ULIF, the evolution of organisms' traits will be eventually subjected to diminished fitness returns. With the diminished fitness returns, for organisms to adapt to a stable environment, they may be subject to selection intensity changes from initially relatively strong positive Darwinian selection to eventual neutral evolution, and meanwhile, mutation rates will be tuned from an initially evolutionary increase under heterogenizing selection to a later decrease due to homogenizing selection. In addition, correspondingly, in evolution rates, organisms will show an initially accelerated evolution to eventual evolutionary stasis (punctuated equilibrium pattern). Conversely, for continuously changing environments, in which new selection pressures may occur frequently, organisms may be subject to phylogenetic gradualism or other possible mixed forms of phylogenetic gradualism and punctuated equilibrium, depending on the frequency of environmental changes. The joint actions of environmental dynamics, selection intensity changes and mutation rate tuning in the context of ecological constraints on individual fitness evolution during adaptation may act as a possible dynamic evolution mechanism to account for the occurrences of diverse evolutionary patterns observed in real organisms, which I refer to as the dynamic evolution hypothesis in this study. The proposal of the dynamic evolution hypothesis may provide important insights to achieve a unified evolution theory.

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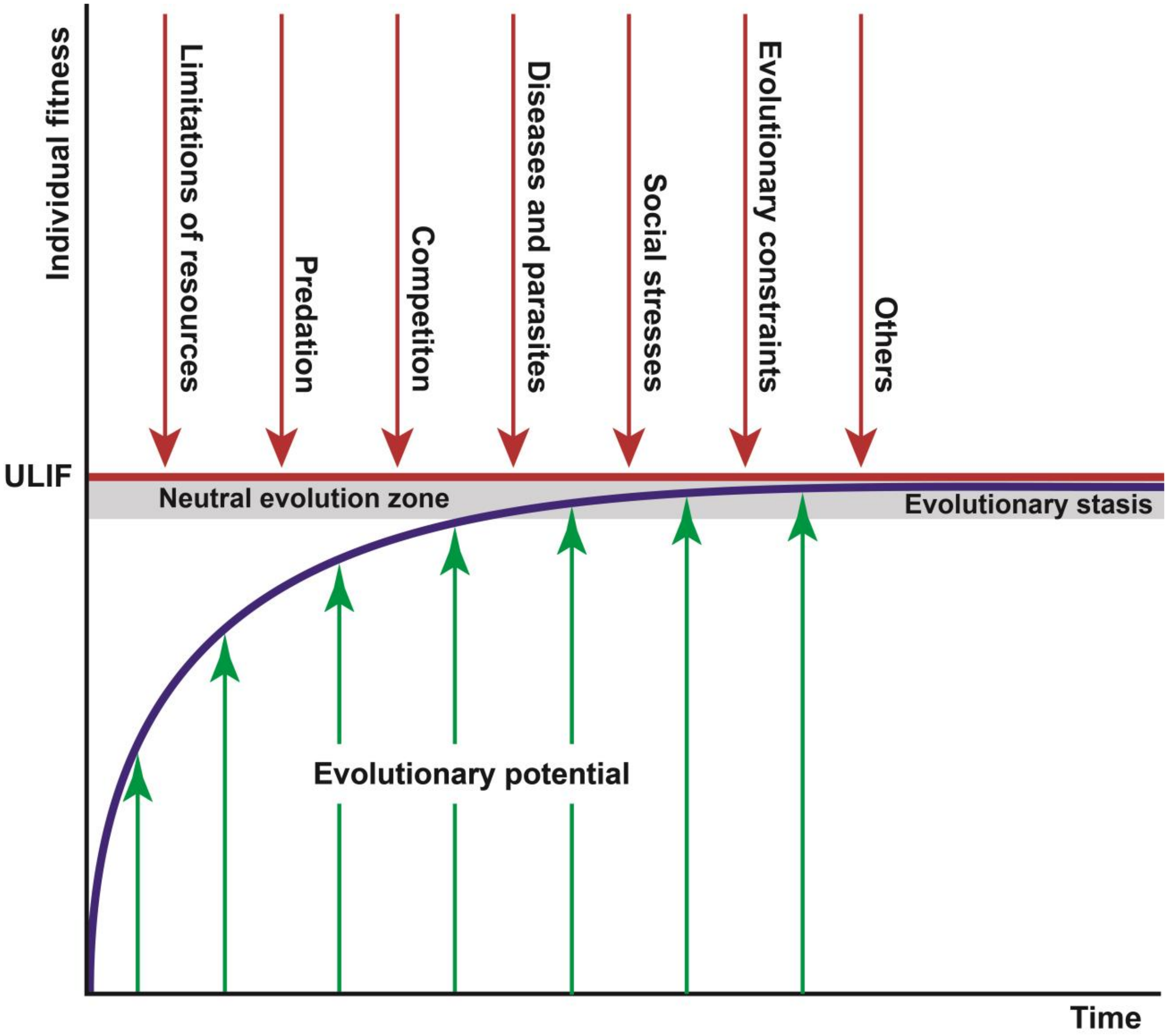

Fig.1 The evolution of individual fitness under ecological and other possible constraints. Adapting to a constant environment (no new selection pressure further occurs), organism's evolution will be subject to an initial Darwinian evolution to eventual neutral evolution and evolutionary stasis due to diminished fitness return and reduced mutation rate mainly stemming from external constraints. ULIF represents the upper limit of individual fitness evolution. Please see main text for details.