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The fitness relativity and path-dependent selection

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ABSTRACT:

Background & Aims: Natural selection assumes that there is an expected fitness advantage (or aim) for any selection of gene mutations or phenotypic characteristics. However, the fitness of the selected gene mutation/phenotypic characteristic might vary as it spreads throughout a population or might vary with changing living environments over both evolutionary and ecological scales. This may result in a “paradox of stationary fitness landscape” in which an expected fitness advantage of a selected gene mutation/phenotypic characteristic might therefore not exist. Based on a dynamic state but not a stationary fitness landscape, we propose that natural selection might exhibit path-dependent selection.

Summary: In path-dependent selection, the gene mutation or phenotypic characteristics are produced completely at random, but some might generate positive feedback as they spread when meeting a specific condition. Such positive feedback also could further facilitate the occurrence of a genetic trait/phenotypic characteristic and the formulation of the evolutionary path. Natural selection will therefore depend on the probability of path, but not fitness value. Analogy to that many paths lead to a bus stop near your office building, the path-dependent selection argues that the shortest or quickest path might be mostly selected, especially when the bus stop is at a fixed location and selection pressure is strong. However, the other paths may also be selected especially when the bus stop could change location or selection pressure is weak. In path-dependent selection, both evolutionary history and distribution of ecological characteristics will greatly affect the evolution of any path. Using this understanding, different pathways can be understood as different points of speciation, where the distribution of species is similar to the peaks of a mountain in which the paths with a high probability will shape peaks, while many other species with low path probability will not separate into other peaks, creating sister species, cryptic species, or redundant species.

Prospects: Path-dependent selection can be described by the complex function, a mathematical method widely used in modern physics. Through complex function, we can describe how multiple factors shape a probability of path-dependent selection in speciation peaks and the oscillation of species peaks. Different pathways, which could also be understood as different dimensional viewpoints, will demonstrate a different understanding of the evolutionary aim of a gene mutation, phenotypic characteristic.

Key words: natural selection; fitness; path-dependent selection; speciation; species diversity

I am, as several other essays emphasize, an advocate of the position that science is not an objective, truth-directed machine, but a quintessentially human activity, affected by passions, hopes, and cultural biases. Cultural traditions of thought strongly influence scientific theories, often directing lines of speculation, especially when virtually no data exist to constrain either imagination or prejudice.

Stephen Jay Gould (Gould, 1992)

In the understanding of either species speciation or selection of the phenotypic traits/behavioral strategies, the modern biological science pre-assumed that any species speciation process and individual behavioral

strategy selection are aimed to achieve a fitness advantage. This methodology of biological study fundamentally is the extension of methodology of physics initiated by Galileo and Newton. The core of Galileo's methodology is “repeatability” of scientific experiments, while Newton logically demonstrated that the “repeatability” is due to the causality between the observed phenomena and the dynamics behind them (Newton, 1729). The “repeatability” and “causality” are consisted the methodological foundation of modern scientific system. The “Invisible Hand” theory initiated by Adam Smith argued that the rationality of human nature, namely the maximization of utility or interest preferences, which is selfishness,

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is the fundamental motivation for human activities (Smith, 1776). While Darwin believed that the fundamental motivation of biological evolution is to improve their fitness, in other words, to reproduce more offspring and survive longer, which is the application of selfishness concept in biological science (Darwin, 1859). Selfishness or and causality are the basic starting point of classical economics and natural selection theory of Darwin.

However, both of these two modern science cornerstones of repeatability and causality meet challenge with the advances of science research. A survey included 1,576 researchers conducted by Nature showed that 70% of the experimental results cannot be repeated, and even 50% of researchers can not repeat their own experimental results (Baker, 2016). In fact, so far, there exist no researcher in the field of physics could completely repeat Galileo's experiment that two iron balls land simultaneously (Cavasinni et al, 1986). Similarly, there are no any researcher in biology field could well get the result of Mendel genetics experiment with pea, in which the ratio (3:1) of red pea to white pea are of a perfect (Fisher, 1936; Mendel, 1925). The scientific experiment advances increasingly demonstrated that "No man ever steps in the same river twice".

Causality, another methodological cornerstone of modern science, also meets a logicity challenge in why human individuals definitely be selfish and why they should maximize their own interests? Richard Dawkins has argued, in the first edition of *The Selfish Gene*, that the fundamental motivation of any biological organisms is to transfer more genes into next generation (Dawkins, 1976). This is of the cornerstone of gene selfishness theory and the kin selection theory. Dawkins (1976) has then further explained the motivation of the selfishness gene, owing to existence of the "replicator" gene, a gene that could control the biological individuals tends to reproduce more of the same copies as themselves. This is a typical philosophy of "Final Cause", which believes that the result is the purpose (or reasons). The unanswered questions of gene selfishness are what drives the birth of "replicators" and why do genes copy themselves instead of mutating to be others? Analogy to Newton at that time, he has attributed the final driving force of the three laws to the God (Newton, 1729), evolutionary biologists could only attribute individual selfishness to poisonous apples, a story of bible (Wang et al, 2021).

In this paper, we here take fitness, one of most basic concepts of evolutionary biology, as an example to illustrate why deterministic causality methodology can only be used to explain the biological phenomena

observed in a static state as Aristotle's and Newton's idea of absolute time. Modern physics methodology of state description therefore, needs to be introduced into the studies of a dynamic fitness landscape. This paper will analyze the fitness in biological evolution from a multi-dimensional perspective or scale, and then try to picture how the path-dependent selection could be evolved in biological evolution and species speciation.

1 The paradox of fitness

In classical evolutionary biology since Darwin, the idea of fitness is used to describe survival rate and reproductive success of biological organisms (Darwin, 1859). Whether a genetic mutation (or phenotypic trait) can be retained in natural selection depends on if they can improve individuals' fitness, which is based on an assumption that there exist an expected fitness of the mutant gene or phenotypic trait (Fig. 1). However, with the diffusion of a mutant gene or phenotypic trait, the fitness of any mutant gene or phenotypic trait will inevitably change with the variation of its distribution density or environment fluctuation (Fig. 2).

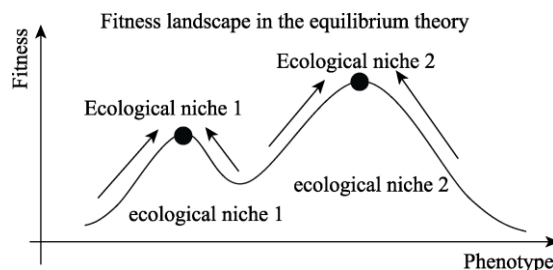


Fig. 1 Fitness landscape in classical theory, in which the fitness of each trait keeps constant, and that the traits with locally maximum fitness become the evolutionary aim.

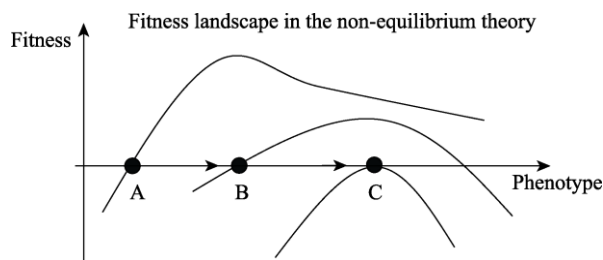


Fig. 2 Fitness landscape in the non-equilibrium theory, in which the fitness of each phenotype might vary greatly. For example, when trait A evolves to trait B who has higher fitness, the individual's fitness with trait A will not increase as expected. This is because the fitness of each trait might vary with the change of population structure and environment.

Fitness might vary with the changing of distribution

frequency of gene (or phenotypic trait) in population, and it might also vary with the change of environment. For example, in classic example of “eagle-pigeon” game, the relatively mild individuals taking a “pigeon strategy” will have a fitness advantage if all other individuals are mild. However, mutated individual with “eagle strategy” will have a fitness advantage compared with others due to its aggression. The gene or phenotypic trait of “eagle strategy” thus will spread. However, with the increasing distribution of “eagle strategy” organisms, the probability of meeting and fighting each other “eagles” will also increase. This will lead to the decrease of their fitness and expected return. Moreover, the living environmental fluctuation might also change the fitness expectation of the individuals with a specific strategy. In harsher environment in which the population would be at a high density and organisms fight with each other more frequently, the probability of choosing “eagle strategy” may get a fitness advantage, or vice versa.

In fact, the expected fitness of mutant gene or phenotypic trait is not constant for any organisms over either time or spatial scales. This is very similar to the situation of climbing a mountain. The peak of mountain (the expected fitness) will be a fixed value in static state. However, in a dynamic state, the climber’s goal (the peak of the mountain) would be uncertain during the process of climbing over the time (e.g., the height of the peak might vary over the time, especially in the geological scale). The distribution of gene or phenotypic trait will not necessarily have a fixed equilibrium point (an evolutionary goal).

In the evolutionary process, some specific mutation and phenotypic traits may have fitness advantage on average. However, the fitness landscape will change accordingly with the change of spatial distribution or spatial location. For example, in the mutually cooperative system between figs and fig wasps, the fig wasps that could pollinate the fig can improve their fitness through the reward of figs. However, the host fig might also sanction the pollinating fig wasps when the number of pollinating wasps entering the figs is too low or too high through fig abortion or constrain the offspring development of wasps (Jander & Herre, 2010; Wang et al, 2015). Moreover, many phenotypic traits with fitness advantage in ecological or spatial scale might not have any fitness advantage over the evolutionary process. For example, peacock’s tail has advantage on sexual selection but may be preyed by predators in evolutionary scale. Thus, there are great differences in the significance of fitness among different scales of observation and understanding.

The different spatial distribution within a population might also lead to very different fitness advantage among the individuals, genetic, phenotypic traits,

whilst the spatial distribution are greatly affected by random effect. In eusociality system of honeybees, the fertilized eggs might be randomly selected by workers putting into queen cell. These eggs will develop into queens, which will have a lifespan more than decades and can almost monopolize the reproduction of the population; However, the life of a workers, which develop in common cells, is relatively short and usually less than a year. Similar to an individual distribution within a population, the species distribution within an ecosystem is also very different among species. Some species that randomly being selected as foundation species might share very much larger population size as well as much longer survival rate than others, and develop into the dominant species. The fitness of such species therefore is much higher than other species within a same ecosystem, without equilibrium point among these species.

2 Time-space superposition and the fitness uncertainty

The distribution of phenotypic characteristics, population size and other ecological processes fluctuate with the variation of space. Similarly, the rate of genetic mutation and the distribution of genetic trait will fluctuate over the time. The fluctuations of those two different dimensions might superpose, and will show complexity such as chaos when they superposed in a nonlinear way. Theoretically, no matter the fluctuation at evolutionary genetic level or the fluctuation of spatial distribution, both of these two fluctuations might lead to huge population change, even might lead to population outbreak or extinction due to the initial value sensitivity. Different trait distribution or genetic mutation rate can lead to unpredictability of population variation through the complexity caused by this nonlinear superposition. With the aggravation of environmental change, the same species in the same region encounter the same new environment may lead to different results: some species grow explosively, and some tend to extinct. Whether a species can survive in the new environment due to the similarity between the new and the past environment they lived. The selection pressure from the past environments shapes the species behavioral tendency and their responses to the new environment (Sih et al, 2011). If the new environment matches the past one, species will adapt well, and vice versa.

In classical studies of evolutionary biology and ecological process, the time scale of genetics and spatial scale of the ecological process are treated as two separate or independent dimensions in most of the

theoretical exploitation. However, in real world of biological evolution, the time scale trait of genetics and spatial scale traits of phenotypic or population distribution might exist interaction effect and genetic effect might not linearly affect the spatial distribution process, presenting more complex effects on each other. One of the possibilities reported in invasion biology is that gene memory of invasion species in past environment matches the current environment and therefore a population outbreak of the invasion species (Ehlman et al, 2019).

In any real biological systems, both time scale of genetics and spatial distribution of organism individuals or species, the genetic inheritance and spatial distribution of the individuals or species are only partial reversible or even not exchangeable, different from the classical theoretical exploitation of complete reversibility. In genetic inheritance, such as plasmid transference, gene jumping and gene recombination, such evolutions are completely nor reversible. It is also true that the spatial distribution of biological trait or the spatial locations (population structure) of individuals or species are also partially reversible or interchangeable. For example, the state located between the queen and the worker bee cannot be completely interchangeable, otherwise the original society will be fluctuated. When both time and space trait are partially irreversible, the genetic inheritance of time scale and spatial ecological distribution could therefore possibly exchange in biological evolution through interaction effect or superposition effect.

The superposition effect (or interaction effect) might be caused through homotropic inheritance or phenotypic plasticity, which plays a bridge between time-scaled inheritance and space-scaled ecological process. Under some environment or spatial distribution, the frequency of some specific phenotypic traits will increase greatly, which could in turn affect the inherited traits of species through phenotypic plasticity and its phenotypic plasticity in space will be transformed into genetic inheritance trait of time scale. On the contrary, if the historical experience matches the environment in reality, the population may dramatically increase and exclude other species (invasive organisms may exclude other local species in a new environment). Homotropic inheritance or phenotypic plasticity might of one of linkages between space and time traits exchange in biological evolution.

3 Path-dependent selection

There is no strict causal relationship between gene and phenotypic trait as well as between phenotypic trait

and fitness advantage in evolution of biological organisms. The loose tie between gene and phenotypic trait means the production of gene mutation or phenotypic trait may exist randomness. Kimura (1983) has stated in neutral theory that molecular mutation may be neutral and random, and gene drift will lead to change of gene frequency. The ecological neutrality theory proposed by Hubbell (2001), which is dynamically the same with neutral selection of Kimura, is well demonstrated in the observation of tropical rain forest; however, neutrality theory meet a difficulty to explain some special heterogeneity of species distribution in other environment like temperate and polar ecosystems in which the abundance of some species is significantly higher than others, but some species are very rare. The neutrality selection theory is based on the assumption that each species in the ecosystem is equivalent, which means that each individual has the same birth rate, mortality rate and migration rate. However, neutrality selection theory (Kimura,1983) meets difficulties in explaining the positive feedback in genetic mutation and the heterogeneity of distribution of gene in cell and the difference of species abundance in ecosystems.

Path-dependent selection suggests that natural mutations or the change of phenotypic trait occur randomly, and some of them can effectively in turn promote the generation of the same mutation or trait in specific conditions, forming positive feedback and promoting the development of the same genetic or phenotypic traits. Another possibility is that the selection from the same external environmental will cause the same mutation more likely. Here, the main point is the occurrence of positive feedback in the genetic mutation or phenotypic traits. This positive feedback may come from some mutant individuals without random mating or with limit local diffusion. Under this condition, some populations with low density may experience rapid increasement when individuals do not diffuse, and thus develop into local populations. Populations with unique trait are formed in a long-time scale, and there exist dispersal and communication among different populations. The frequency of their diffusion and communication will determine whether they can form local population with new traits.

Similar to the dispersal process of seeds, a few fluttering seeds can fall on suitable environment. These seeds may change the surrounding environment with their growth, making it easier for themselves, their offspring and other seeds to grow, and therefore gradually develop into a new population even a new ecosystem. Biological organisms are inclined to live in the environment that is matched well to the past

environment due to inherent inertia and genetic factors, which will strengthen the positive feedback, and create an environment more conducive to the survival with same trait or the occurrence of similar mutations. Similar to the development of technology and the occurrence of new scientific theory, when someone generates a thought or technology, the thought should be appreciated by others, and technology should meet an enterprise or society in need. Then, the participation of others will further improve the thought and technological system. The system formed by positive feedback will accelerate the dissemination and application of theoretical thought and technology (Wang et al, 2021).

Path-dependent selection will focus on the frequency of evolutionary paths rather than regarding fitness as the purpose (or aim) of evolution. Similar to the path from a bus stop across grassland in front of the office building, there will be plenty of trodden paths. Some of these paths, such as the shortest path in distance or the quickest path in time, might be mostly selected because a lot of pedestrians get through these paths. However, some other paths could also be selected though they may be seldom selected, especially in the case of the bus stop changing with its sites. Natural selection might select multiple paths rather than the optimal one under the limited selection intensity. Some paths are selected more frequently, while others are less. With the increase of selection pressure, the frequency of the selection on optimal path may increase. In this framework, natural selection means a selection path probability. In other words, each path has the different existence possibility.

In path-dependent selection, the superposition of time-scaled inheritance and space-scaled ecological process plays a significant role in the path formation of speciation or genetic inheritance. When species enter a new fluctuating environment, they constantly match the new environment with their past experience or gene memory in the adaptation of fluctuation of environment. The reaction, which can be regarded as evolution, will change the environment (including biological environment and abiotic environment), which in turn will further affect the species themselves. Such positive feedback makes paths emerge more easily.

The positive feedback of population growth may also come from the initial physiological or behavioral response in a specific environment, which might lead this response more adapted in some cases, and such response could even transmit to the next generation (Donelan et al, 2020). In the early stage of evolutionary path, the environment encountered

randomly by species has a great impact on the evolution path of species (Blount et al, 2008). In other words, the random environment in the early stage of evolution will greatly determine whether the path could be evolved. After path establishment, the environment will have less effect on the path formulation because it needs large exit cost or sunk cost to transfer to other paths, which will lead the path being locked. Under such condition, path-dependent natural selection may not be a global optimal result, but a sub-optimal result (or a near local-optimal result). Furthermore, if the new environment does not match the past path of species, they would be extinct or start a new path.

The entropy flow in the system will greatly affect the number of paths in the system (Bertola & Cafaro, 2008; Gallaavotti, 2012). With large entropy flow, the system allows a lot of paths and the randomness will have important influence on the selection in evolution of path, which is similar to neutral theory (Ludovisi, 2006; Lin, 2015). For example, the leaf may move randomly in the direction of the river transversal when someone throw it in a wide river. But the leaf may seldom move along the river transversal when it appears in a narrow river. In ecosystem with large entropy flow, such as tropical rainforest, the flow of energy will large and the distribution of species will be close to neutral theory. In this condition, the strength of nature selection will be weak. When the entropy flow is small, there will be only a few evolutionary paths and the species may have more chance to choose the optimal path in the theory of nature selection (Ludovisi, 2006; Lin, 2015).

4 Transition probability of paths and species diversity

Based on the static fitness landscape, Traulsen et al (2007) suggested that the evolution of phenotypic trait from one state to another is along the path with shortest in distance or fastest in time, thus there exist the so-called optimal evolutionary path. Under this condition, there may be multiple possible paths in natural selection, and the path with the shortest time will be naturally selected in the long run. However, the fitness landscape is not static in most of cases, the fitness may change with the frequency variation of the spatial distribution of its characteristics (Li et al, 2021) (Fig. 2). In this case, the optimal path with shortest distance or fastest time may not be achieved because there may be no fixed goal in evolution.

At point A of the dynamic fitness landscape in Fig. 2, the species evolve to point B with larger fitness. However, when it evolves to the point B, the variation

population structure will lead to the change of the fitness landscape, and the fitness does not increase as expected. This is because the phenotype in the finite population is affected by both random drift and selection in evolution (Ewens, 2004), and its fitness will thus change. Take the evolution of cooperative strategy in the population as an example, its fitness is expressed as: $f_i = 1 - w + wF_i$, where w represents the selection intensity (Li et al. 2021), F_i represents the benefits of the strategy A in the game, and F_i is a function of its frequency. Fitness depends on selection intensity and population density, which change almost all the time in population evolution, and fitness landscape therefore changes accordingly. Taking the frequency of the phenotype A, its frequency is x_0 at time t_0 , x_n at time t_n , through the time point t_k , the frequency is x_k . Note that the probability from x_1 to x_k is $P_{x_1x_k}$, the probability from x_k to x_n is $P_{x_kx_n}$, and the probability from x_1 to x_n is $P_{x_1x_n}$. Thus, $P_{x_1x_kx_n} = P_{x_1x_k} P_{x_kx_n}$. During the evolution of the phenotype A from x_1 to x_n , the frequency x_k may refer to many values. Therefore,

$$P_{x_1x_kx_n} = \sum_{x_k} P_{x_1x_k} P_{x_kx_n}$$

When measuring the frequency of each generation,

$$P_{x_n|x_1} = \sum_{x_1} \sum_{x_2} \dots \sum_{x_{n-1}} P_{x_1x_2} P_{x_2x_3} \dots P_{x_{n-1}x_n}$$

The distribution of each generation becomes a series of values on continuous variables. Then, we have the transition probability from x_0 to x_n , which is obtained by the sum of all paths evolved from x_0 to x_n , and the sum is replaced by the integral:

$$f(x_n | x_0; t) = \iint \dots \int f(x_1|x_0; \delta t) f(x_2|x_1; \delta t) \dots f(x_{n-1}|x_n; \delta t) dx_1 dx_2 \dots dx_{n-1}$$

$f(x_1 | x_0; \delta t)$ refers to the transference probability of the state x_0 to x_1 evolving from the previous generation to the next generation, and the rest can be done in the same manner.

Through the formula above, the probability of evolution from the frequency x of phenotype A to other state over a period of time can be calculated, which is the sum of all possible path between the two phenotype values. Combined with the phenotype distribution at the initial time, the new phenotype appears with different path leading to current phenotype distribution.

Besides, the coexistence of multiple phenotypes can be observed at a certain time by means of the phenotype distribution. The phenotypes with high frequency can be considered as successfully differentiated phenotypes and can be used as the basis for species determination (species definition based on

phenotypic characteristics) if they meet the statistical quantitative relationship (reflected in small density difference and large phenotypic difference). According to the concepts above, we can define the species identification: in statistical analysis for multiple variables of the level of biological characteristics of either genetic characterization, morphological characteristics, or ecological process between two populations. When the time of the species differentiation for two or more dimensional variables is long enough, if the distance of them between populations is longer than the variance of variables within the population, the individuals with corresponding variables belong to different species; however, if only one independent variable satisfies this condition, the individuals with the corresponding variable belong to a species variety (Li et al, 2021).

As stated in the above definition, not only phenotype, genotype, ecological process but even species also might be of path-dependent evolution process. Multiple paths will evolve starting from a state, and these paths will be fed back by the frequency. In the later stage of evolution, if the effect impacted by the environments is small, the paths will be fixed more probably, and it is difficult to transfer among paths. Unless the environment fluctuates violently, the phenotype begins a new round of evolution. Phenotypes depending on the paths can evolve significant characteristics more easily, and speciation will be more likely. In addition, each evolutionary path has its own probability. When the selection intensity is limited, multiple paths with higher frequency are allowed to exist, and therefore species diversity will be easier evolved. The path dependent selection therefore might well explain why some phenotypes with low fitness or even not fitness could be observed in real biological organism and ecosystems.

Under a certain selection intensity, the existence of evolutionary paths with different probabilities shows the continuity and discrete among species, which provides a theoretical explanation for the coexistence of different species. A large number of species on the path with high probability exist in nature, forming independent species in the evolutionary tree. While the species on the path with lower probability can be regarded as sister species, sympatric species, or even redundant species. That is because that the statistical characteristics of the frequency distribution between these species and the independent species do not meet the conditions in the species definition. This gives rise to the conceptual diagram of species distribution (Fig. 3).

5 Complex function in theoretical biology

Observation results such as fitness realization or characteristics

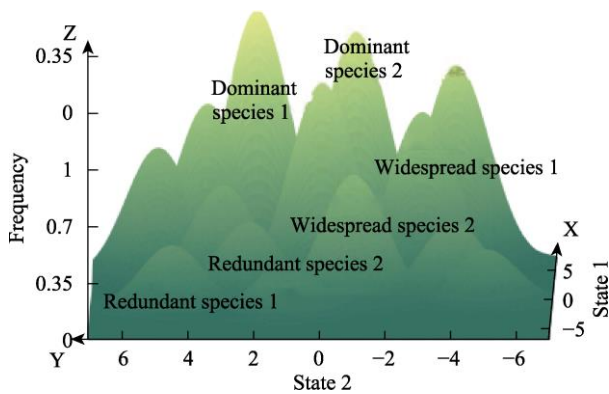


Fig. 3 Conceptual diagram of species distribution. In path-dependent speciation, the shaping of species peaks at a specific time will depend on the probability of its evolutionary path. The continuous mountains and the independent peaks represent the continuity and separation of species, respectively.

expression are often regulated by multiple factors or even antagonistic effects. In genetics, most of the phenotypic characteristics are also regulated by multiple alleles. According to the genetic linkage separation theorem, two alleles, A and a can lead to four combinations: AA, Aa, aA, aa. Aa and AA correspond to dominant characteristics, and aa corresponds to recessive characteristics. Both Aa and AA show dominant phenotype and cannot be identified by the nature. However, in inheritance, AA provides two dominant genes A, Aa only provides one dominant gene, and this difference can only be reflected in the future. This evolution might be well described by a complex function.

The complex number is composed of real number and imaginary number, which are usually written in the form of $a + bi$. Both a and b are real numbers, and i is an imaginary number defined as the square root of -1 . In dynamic process, the imaginary part can be expressed as the future or past state, which is covered by the current time (the real part), and it will appear only with the continuous evolution. Based on argument principle, a complex phase to represent the fluctuation of biomass. Genes and phenotypic characteristics can be explicitly expressed as oscillations of complex functions. These two dimensions can be interdependent but evolve in parallel according to certain rule. By introducing the complex function, both genotype and phenotype dimensions are included into the evolution equation, and they are connected by the relationship between the real and imaginary part of complex function. The frequencies of male and female parent genotype (corresponding phenotype) are $a + bi$ and $c + di$ respectively, and their real and imaginary parts

correspond to the frequencies of dominant and recessive genes respectively. Taking the algebraic structure of complex numbers into simple multiplication rule, the transference of genes between two generations: $(a + bi) * (c + di) = (ac - bd) + (ad + ba) * i$. The real parts a and c of parents have an impact on the both real and imaginary parts of offspring.

There are similar effects between genetic factors representing time effect and population distribution representing spatial effect in evolution. The population distribution in space must be affected by historical genetic factors, and cannot be considered by simply adding up. Therefore, if the contributions of inheritance and phenotype dimensions are considered simultaneously with the mapping relation between them, a time-dependent complex function to describe the evolution process over time will be more reasonable.

6 Separation vs. Continuity and Discontinuity vs. Balance in evolution

The paths of evolution contain discreteness and continuity in different research scales. Separation is a prerequisite for the stability of species. Meanwhile, species formation can also be a continuous process (Wang et al, 2020). The Darwinian natural selection theory holds that natural evolution is gradual and continuous, and the mutation rate is fixed parameter (Huxley, 1944). This theory cannot explain explosion of species, and why different evolutionary branches have evolved a large numbers of species, but some branches almost stop species generation (Gould, 1989). Darwinian natural selection also could not be able to explain how unique characteristics evolve in a continuous evolution process.

In “Punctuated Equilibrium” theory (Eldredge & Gould, 1972; Gould & Eldredge, 1977), new species can only emerge by branches. Once formed, new species will be in a state of conservation or evolutionary stagnation and keep their features significantly in phenotype until next evolution step. “Punctuated Equilibrium” theory explains the dis-continuousness of evolution in which species can only be evolved between jumping and stagnation, instead of being smooth and gradual speciation.

Path-dependence selection might well integrate Darwin’s natural selection and “punctuated equilibrium” theory, differing in driving forces between these theories under path dependent selection scenario. There are three elements included in evolution: replication, mutation and selection (Nowak, 2006). Specifically, biological organisms tend to

replicate the characteristics and genes with high similarity, evolving through the original path. In addition, organisms can mutate and preserve more competitive characteristics and genes, which can generate new paths. These two processes antagonize each other by selection and can form several independent evolutionary paths. Mutations usually occur in a fixed proportion during replication, in contrast, replication may change with the external environment. When the environmental capacity is large, the frequency of replication will be high, and the number of replication can be much greater than mutations. This leads to the domination of replication in evolution, and mutation is merely the fine regulator. Thus, the evolution shows gradual and continuity.

When the capacity of the environment reduces, the difference between replication and mutation will also reduce. These two forces therefore will confront strongly, and the system be at the critical point. When one force is defeated, the dominant factor will transfer from one to the other in evolution. Thus, “mutation” will occur in morphology, and the evolution shows discontinuous. Due to the fluctuation of environment and the change of replication and mutation themselves, the evolution is usually the alternation between discontinuous and continuous processes, and can be explained by the path in evolution, which depends on the distribution of the evolutionary path branches at the current and adjacent time points. Overall, it is necessary to notice that continuity and separation are opposite concepts.

7 Different observation dimensions, scales, views might get different results

Path dependent selection might provide an explanation why the understandings and conclusions for the same phenomenon might differ, and even contradictory, in different dimensions, observation angles, views or observation scales, existing different schools in understanding the same observations. In the evolution process, different time points and spatial positions may evolve different dimensions and therefore different pathways. Different paths have different evolutionary “purpose” or “aim”, and therefore different conclusion or understandings.

In the exploration of the evolution of cooperation, there also exist two schools on whether the conflict directly exist in the cooperation systems, especially in the altruism systems. These arguments also exist in the exploration of fig-fig wasp mutualism (Herre & West, 1997; Wang et al, 2008; Wang, 2011). According to the macro-level observation of behaviors, pollinating wasps with unique pollen baskets collect

pollen without feeding on themselves and then enter the figs to pollinate the fig and then oviposit their eggs. This is the typical altruism. The fig provides part of female flowers for the wasps to oviposit, and their larvae feed on ovary to develop. After developing into wasps, they collect pollen and spread the pollen. The more pollinating wasps, the more seeds of figs and larvae. In the perspective of interest exchange or macro-level observation, figs and fig wasps is of the mutual cooperation (Bronstein, 2001).

However, observations of individual wasps showed that a few wasps are lack of pollen baskets or behaviorally cheating not carrying pollen in their pollen pockets. In fig-fig wasp interaction, there is also exist positive fitness interaction presenting a cooperation and also negative fitness interaction presenting a conflict in literatures (Bronstein et al, 1996; Herre & West, 1997). However, the experimental data of fig-fig wasp mutualism in China showed that both cooperation and conflict interaction exist, depending on the availability of the common resource (Wang et al, 2008) and that fig-fig wasp interaction might fluctuate over the time and spatial variation (Wang et al, 2011; Wang, 2022).

Adam Smith and Darwin have realized that that the assumptions of the selfishness human being or fitness of natural organisms have difficulty in explaining some observations in both human being and natural organisms. From the macro perspective of society or population, the selfishness (or rationality) could well explain the observations individual behaviors. However, at the individual level, both Adam Smith and Darwin have noticed some altruistic behaviors contrary to selfishness and rationality. In *The Theory of Moral Sentiments*, Adam Smith mentions that human being was a high-level creature who should share both morality and selflessness.

Darwin has also realized that the “survival of the fittest” theory could not be able to explain all biological phenomena. In nature, many insects with social characteristics can give up their reproduction and even sacrifice their life to help other individuals. The survival of the fittest cannot explain these altruistic behaviors. He therefore, stated in *On the Origin of Species*: “I am convinced that Natural Selection has been the main but not exclusive means of modification” (Darwin, 1859).

Different researchers might have different understandings on human nature or motivations of biological evolution due to their different experience and knowledge backgrounds, or even have huge differences in different stages of growth of the researcher. In fact, these differences constitute the differences on dimensions or evolutionary paths on a

smaller scale, which cannot be distinguished by our observation or detection means. Many totally different conclusions, such as the ecological roles of redundant species (Walker, 1992), might come from improvement of research methods and technologies, that is, the improvement of detection technology. From the perspective of static spatial effects, redundant species have almost no ecological impact on the ecosystem, similar to that appendix was considered to be a degenerative organ in the process of biological evolution without any functional significance in the past. However, in the evolutionary history of the ecosystem, redundant species may play an extremely important role. When the ecosystem collapses, redundant species may become crucial in reconstructing a new ecosystem. Similar to the function of the appendix of human body, the modern research of immunology showed that appendix is important in immunologic function (Bollinger et al, 2007).

8 Discussion and Conclusion





In fact, neutral selection theory assumes that gene mutation, (or the generation of traits, behaviors and even species) in biological evolution are completely random without directionality. However, in real biological systems, the distribution of the observed traits, behavior characteristics and species are not completely uncertainty. In many cases, some traits and behavioral characteristics have significant dominant, and some species occupy a dominant position in ecosystems, but their traits, behavioral characteristics and species are very diverse. The contradiction between the dominant distribution of a specific traits/behavioral characteristics and the species/genetic/phenotype diversity can be reconciled by path-dependent natural selection mechanism.

Path-dependent natural selection argues that there is randomness in gene mutations or the generation of traits, behaviors and species. However, under certain conditions, these gene mutations or traits, behaviors and species have formed positive feedback and their paths. New environment will cause significant impact on evolution path of the species, but after the establishment of the path, p , the fluctuations of the environment will have a less impact on the path, because the transference to another path needs great exit cost or sunk cost at this time. However, due to the information exchange or path exchange among paths, there is still probability transference. Therefore, there will exist both path separation and continuity among paths, which will evolve into a mountain path map, and each path resemble to a mountain peak. The heights of peaks in the path will change and even

exchange roles with each other with variation of time and space. The different paths could also be understood as a specific gene mutation, behavioral trait, species evolution might present a different fitness in different dimensions.

In path-dependent natural selection, the natural selection will favor those gene mutations, behavioral traits or species that can improve their fitness instantaneously rather than those in the long term. The path-dependent natural selection would strongly depend on the paths they have experienced in history, and the selections are of path frequency rather than fitness advantage. The higher frequency of the paths, the higher tendency it is to be selected. Similar to the paths chosen by individuals of human beings, the paths we often choose in many cases are paths that more people worked, but not shortest or most efficiency paths. In natural evolution, the optimal evolutionary paths might therefore not exist and the multiple paths might coexist, due to that the purpose (or aim) of evolution of the organisms might change with the variation of environment or population structure. In different paths, the relative fitness (or aim) of biological individuals (or species) will be different.

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