Li et al. *Zool. Res. Divers. Conserv.* 2024, 1(2): 133−140
https://doi.org/10.24272/j.issn.2097-3772.2023.202

ZRDC Zoological Research: Diversity and Conservation

Article Open Access

Path-dependent speciation in dynamic fitness landscapes

Min-Lan Li[1,2,#], Chao Wang[1,#,*], Rui-Wu Wang[1,*]

[1] *School of Ecology and Environment*, *Northwestern Polytechnical University*, *Xi'an*, *Shaanxi* 710072, *China*
[2] *School of Mathematics and Statistics*, *Northwestern Polytechnical University*, *Xi'an*, *Shaanxi* 710072, *China*

ABSTRACT

Species is a fundamental concept in evolutionary biology and biodiversity. However, existing species definitions are often influenced by artificial factors or are challenging in practical application, leading to confusion in species classification. Due to uncertain environmental changes and random genetic drift, the fitness expectations of a population may shift, causing species to evolve to a new evolutionary state based on their current instantaneous fitness within a dynamic fitness landscape. This contrasts with the classic static fitness landscape, where fitness expectations are constant. In a dynamic fitness landscape, speciation may exhibit path dependence, where the evolution of traits follows a probabilistic path, creating feedback that shapes evolutionary trajectories. The path-dependent evolutionary mechanism suggests that species survival within an ecosystem is not directly determined by their fitness but by the probability of their evolutionary pathways. This model also indicates that species can coexist with varying probabilities under limited environmental pressures. Consequently, new species, cryptic species, or sympatric species may emerge via path-dependent evolutionary processes. Within this framework, we developed a mathematical species concept, which may guide future species classification methodologies.

Keywords: Biodiversity; Ecological/evolutionary model; Fitness landscape; Stochastic process; Path dependence

INTRODUCTION

Since the publication of On the Origin of Species (Darwin, 1859), at least seven species concepts have been proposed, including the biological (Mayr, 1942), ecospecies (Van Valen, 1976), morphological (Cronquist, 1978), evolutionary (Wiley, 1978), phylogenetic (Eldredge & Cracraft, 1980), and taxonomic (Mayden, 1997) species concepts. However, no definition has been able to clearly delineate a species (De Queiroz, 2007; Liu, 2016; Mallet, 1995), and no single biological characteristic, including reproductive isolation, can reliably distinguish one species from another (Wang et al., 2020; Wu et al., 2020). Traditional species definitions view the speciation process as non-dimensional, lacking consideration for time and space scales (Bock, 2004). These non-dimensional definitions presuppose that each variable of any biological trait confers a distinct fitness advantage and may occupy a specific niche within a species community, constituting the fitness landscape (Frank, 2011; Wright, 1932). The fitness landscape is also often depicted as a multi-dimensional surface with distinct fitness peaks and valleys (Steinberg & Ostermeier, 2016).

The constant fitness expectation of any biological characteristic may be unreliable because the evolution of such characteristics may simultaneously alter fitness expectations over temporal and spatial dimensions. During the evolutionary process, environmental selection pressures frequently influence adaptations, while those adaptations concurrently reshape the environment. Populations moving across a fitness landscape also alter the landscape (Nowak & Sigmund, 2004). Therefore, a constant fitness expectation cannot be anticipated in a dynamic fitness landscape, as species evolution continuously alters fitness expectations.

In a dynamic fitness landscape, the selection of one or more biological characteristics may be determined by the instantaneous fitness landscape at each evolutionary step. Consequently, the evolutionary process tends to move towards increased fitness in the instantaneous fitness landscape. The selection of evolutionary characteristics or strategies in such an uncertain fitness expectation heavily depends on their evolutionary history or environmental contingencies (Gould, 1977). These characteristics or strategies may generate feedback, altering the state's fitness in a population and forming an evolutionary path (Arthur, 1989; Wang, 2021; Wang et al., 2022). This paper discusses how species are shaped by the probability of evolutionary path selection under a dynamic fitness landscape framework,

Received: 18 January 2024; Accepted: 05 February 2024; Online: 02 July 2024

Foundation items: This work was supported by the NSFC-Yunnan United fund (U2102221) and National Natural Science Foundation of China (32171482)

[#]Authors contributed equally to this work

*Corresponding authors, E-mail: chaowang@nwpu.edu.cn; wangrw@nwpu.edu.cn

considering characteristic variations across several dimensions.

MODELS

Fitness landscapes and evolutionary pathways

Fitness can be conceptualized as the frequency of a certain state's descendants. Therefore, for simplicity, the distribution of any biological characteristic, such as genotype (Nowak, 2006) or niche (Schwilk & Ackerly, 2005), can be approximately treated as the fitness landscape. A stationary fitness landscape is independent of the time scale, such that it remains constant during the evolutionary process unless the environment poses a novel or extreme challenge (Frank, 2011). Typically, fitness f of phenotype x obeys a normal distribution with mean $\bar{x}$ and variance σ^2 in a unimodal stationary fitness landscape, which can be expressed as

$$f(x) \triangleright \left(\bar{x}, \sigma^2\right) \tag{1}$$

Clearly, phenotype $\bar{x}$ is optimal. Based on the stationary fitness landscape assumption, Traulsen et al. (2007) proposed that the optimal evolutionary trajectory between two species is represented by an exponential function.

Nevertheless, in a multipeak fitness landscape, as shown in Figure 1, a population with a lower average phenotype will evolve in the direction of improving fitness to increase its fitness during the evolutionary process (Frank, 2011; Smith, 1982; Traulsen et al., 2007; Whitlock et al., 1995). One unresolved issue is how populations shift from a lower fitness peak to a higher fitness peak, crossing a valley that temporarily reduces population fitness, which contradicts the principle that natural selection follows a path of increasing fitness (Coyne et al., 1997; Frank, 2011; Nowak & Sigmund, 2004).

Frank (2011) proposed the concept of the "reaction norm", which is the probability of expressing phenotype x given a genotype with an average phenotype $\bar{x}$. This concept has the potential to smooth a multipeak fitness landscape into a single peak landscape, providing a directly increasing path of fitness to the highest peak, which depends on the nature of the fitness surface and the reaction norm (Frank, 2011). After smoothing a multipeak fitness landscape, the evolutionary dynamics resemble those of the original single-peak fitness landscape (Figure 1). However, this approach overlooks that the fitness landscape is continually changing, even in the absence of novel environmental challenges. A fitness landscape may experience simultaneous changes in fitness across both temporal and spatial scales. Temporal changes reflect environmental variations impacting the fitness landscape, while spatial changes result from individual interactions affecting trait distributions within the population, which, in turn, influence the fitness landscape. Multiple dimensions, beyond the spatial distribution of a single genetic or phenotypic trait, may shape the multipeak fitness landscape.

To illustrate the evolutionary dynamics in a varying fitness landscape, without losing generality, we use the evolutionary trajectory of the phenotype as an example, although similar evolutionary processes apply to other characteristics. As a population evolves, its average phenotype changes based on the current fitness landscape. This occurs because individuals in a population are randomly chosen to die and, with certain probabilities, generate mutations or produce offspring identical to themselves. By understanding the evolutionary mechanism, we can determine these probabilities. Random drift and environmental changes, including the natural environment and individual interactions, continuously alter the population configuration. Further details on this process are provided in the following context. Repeated application of this approach leads to the emergence of various paths with differing probabilities over time, resulting in minor adjustments to the average phenotype. When selection pressure is weak, numerous trajectories are possible, but only one trajectory is feasible under strong selection pressure. By examining the probability distribution of these trajectories, we can identify the paths a population takes due to natural selection and random drift. If we consider the evolutionary process in terms of species, one average phenotype may diverge into two or more average phenotypes. It is consistent with Darwin's assertion that evolutionary history has shaped contemporary biology (Darwin, 1859; Wang, 2015). From this perspective, it is evident that speciation is path-dependent (Wang, 2021; Wang et al., 2022).

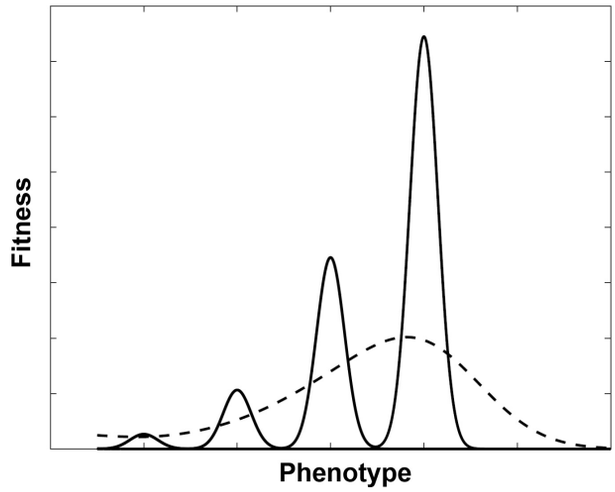

Figure 1 Fitness landscape of phenotype (Frank, 2011)
Solid line represents fitness landscape for each phenotype corresponding to natural conditions. When a population evolves on such a multipeak fitness landscape, it can easily become trapped at a lower local peak. Dashed line represents single-peak fitness landscape obtained by smoothing the multipeak fitness landscape, making it easier for any phenotype to evolve to a higher fitness.

Contrary to the traditional view that the fitness landscape is a static ground over which the population moves (Frauenfelder & Leeson, 1998; Sherrington,1996; Wright, 1969), populations actually evolve based on different instantaneous fitness landscapes in a dynamic fitness landscape. This dynamic fitness landscape can be described as a set of functions

$$\left(f(x(t_1)), f(x(t_2)), f(x(t_3)), \ldots, f(x(t_n))\right) \tag{2}$$

where $f(x(t_i))$ denotes the instantaneous fitness distribution at time t_i and $x(t_i)$ is the state at time t_i. Each instantaneous fitness distribution may differ from the others. In the case of a stationary fitness landscape, we have

$$f(x(t_1)) = f(x(t_2)) = f(x(t_3)) = \cdots = f(x(t_n)) \tag{3}$$

We focus on the concept of evolutionary trajectory within a dynamic fitness landscape. Consider a state evolving from value x_0 at time t_0 to value x_i at time t_i, represented by the

path $x_0(t_0), x_1(t_1), x_2(t_2), \ldots, x_n(t_n)$ (Figure 2). By tracking all possible paths in this population, the probability of the described path can be denoted as $P[(x_0(t_0), x_1(t_1), x_2(t_2), \ldots, x_n(t_n))]$, which indicates the transition probability that the average value of a state in a population evolves from x_0 to x_n passing through $x_1, x_2, \ldots, x_{n-1}$ within $t_n - t_0$. Specifically, a population with a globally dominant state, such as phenotype x_i, affected by random drift and natural selection, will evolve to one with several locally dominant states (including the original state) with varying probabilities according to its instantaneous fitness landscape. These evolutionary paths, representing evolutionary history, determine the current distribution of species. Figure 2 illustrates several paths that can depict the evolutionary process. Note that the fitness distribution remains non-varying over a very short evolutionary period or within a stationary fitness landscape.

It naturally follows that the evolutionary path favored by natural selection has the highest probability. In a stable environment with limited pressure, multiple paths coexist with varying probabilities. Even when the environment presents novel or extraordinary challenges, numerous paths remain available. However, in the extreme case of continuous, intense environmental pressure, only one path is possible. Species have emerged along these evolutionary paths. In the following sections, we discuss how species develop and how to distinguish between them based on the evolutionary paths of their biological characteristics.

Speciation dynamics in evolutionary pathways

As the population moves along evolutionary paths within the dynamic fitness landscape, a population with a certain average phenotype will differentiate into multiple subpopulations with distinct average phenotypes. This differentiation is driven by individual interactions and environmental fluctuations, leading to the emergence of new species. Defining the function $\mathrm{P}[\mathrm{x}(t)]$ as the probability of an evolutionary trajectory, where the path $\mathrm{x}(t)$ is the independent variable, indicates the transition probability by which a state evolves into another over a given period. Index x can label various properties within the set, such as allele frequency, genotype, phenotype, or group of individuals (Frank, 2011). Given that previous research has primarily focused on the biological characteristics of phenotype and genotype for species delimitation, we also selected them as the described objects in the present work, while acknowledging that other biological characteristics can be equally selected. A population with an average phenotype x_0 will eventually evolve into two subpopulations with average phenotypes x_k and x_k' (two phenotypes at time t_k). If the distribution of these phenotypes satisfies specific criteria, new species will then arise.

To illustrate the evolutionary path and investigate the influence of selection intensity, a Monte Carlo simulation of the Moran process is introduced to visualize the evolution of average phenotypes (or genotypes) in a population. In the frequency-dependent Moran process, an individual reproduces with a probability proportional to its fitness and replaces a randomly chosen individual (Claussen & Traulsen, 2008). The transition probabilities thus include heredity ($P_{i,i}$) and mutation ($P_{x_i,x_{i+1}}, P_{x_i,x_{i-1}}$), where x_i represents any biological characteristic such as phenotype, genotype, allele frequency, or species. The evolutionary process is simulated by focusing on the frequency of the cooperators in the snowdrift game, in which cooperation yields a benefit b to the cooperator and the opposing player, and incurs a cost c if the opponent defects, but only a cost $c/2$ if the opponent cooperates. Fitness is denoted as f_{x_i} and g_{x_i} for cooperators and defectors, respectively. The effect of selection intensity is also considered, where fitness becomes

$$f_{x_i} = 1 - w + wF_{x_i},\ g_{x_i} = 1 - w + wG_{x_i} \tag{4}$$

with w representing selection intensity and

$$F_{x_i} = (b - c/2) \times x_i + (b - c) \times (N - x_i),\ G_{x_i} = b \times x_i. \tag{5}$$

Figure 3 presents the evolutionary process of the average phenotypes over time, assuming an initial average phenotype of 50. The three-dimensional diagram shows the evolutionary path space under moderate selection intensity. It is evident that there are multiple paths from the initial state to the final state. The fitness landscape at each time is shown by the frequency distribution of phenotypic values. As seen in the upper left-hand corner of Figure 3, the distribution curve is unimodal at the initial time, becoming bimodal at time 200. The average phenotypic values cluster around 51 and 57, indicating divergence of the optimal phenotype. We can further assess whether individuals with these two phenotypes

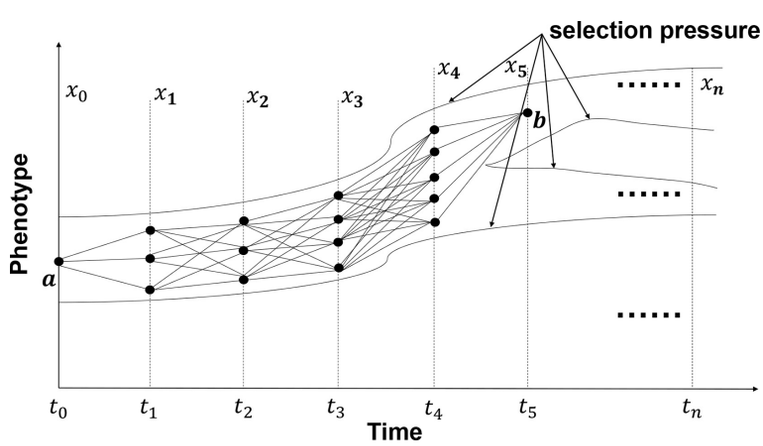

Figure 2 Evolutionary process for a phenotype from *a* to *b*

A phenotype can evolve into the same or a different phenotype at each time step, based on a certain probability determined by its instantaneous fitness. This process can result in the emergence of many paths. Suppose a trajectory consists of phenotype $x_0, x_1, x_2, ..., x_n$, then its probability is $P[x_0(t_0), x_1(t_1), x_2(t_2), \ldots, x_n(t_n)]$. Under moderate selection pressure, multiple evolutionary paths can exist. Over time, phenotype differentiation causes these paths to diverge.

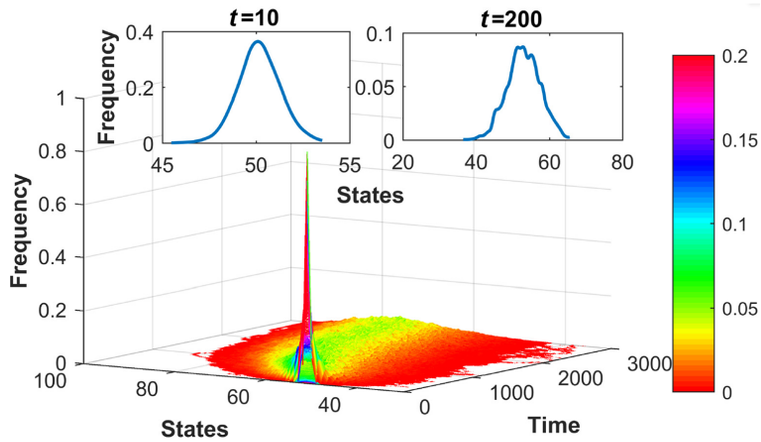

Figure 3 Path-dependent evolutionary process of states

The three-dimensional diagram illustrates the evolutionary path space of the state under moderate selection intensity. The state may represent genotype, phenotype, or ecological process. The frequency distribution curve of t=10 is shown in the upper-left corner. The frequency distribution curve of t=200 is shown in the upper-right corner. From the perspective of phenotype, the distribution curve transitions from unimodal in the early phase to bimodal at t=200, indicating that the phenotype differentiates from one phenotype (50) in the initial stage into two phenotypes (51 and 57) at t=200. This enables us to determine whether the species with phenotypes 51 and 57 are different species.

are the same species based on their relationship. The frequency distribution at different times may show either a single-peak or multipeak distribution. When multiple local dominant phenotypic values are present, the differences between describe the discontinuity between species, while the variance reflects continuous differences with species.

As presented in Figure 3, when selection intensity is limited, a population evolves not only along the path with the greatest probability but also along other paths with lower probabilities. It is crucial to distinguish species within this framework. According to the morphobiological species concept proposed by Hong (2016), a species is a biological group composed of one or more natural populations, exhibiting polymorphism and continuity of variation in morphological traits within the species, while there are two or more independent or statistical interruptions in the variation of morphological traits between species. Based on the polymorphism and continuity of variation of morphological traits within species, as outlined in Hong (2016), we must focus on phenotypes with high fitness and variance to discuss the nature of species.

An important question arises: how can we determine the relationship between the discontinuity of different phenotypic values and their variance in the context of path-dependent speciation to distinguish species? Based on the evolution trajectories that populations follow with varying probabilities under the influence of natural selection and random drift, we mathematically discuss the conditions for speciation and define the concept of species.

RESULTS

Conditions of speciation

The concept of path-dependent speciation provides novel insights into the mechanisms of species evolution and the formation of new species. Here, we introduce a mathematical approach for species delimitation based on path-dependent speciation. We consider two biological characteristics, C_1 and C_2, of an original species. As shown in Figure 4, the emergence of a new species depends not only on the degree of differentiation of these two characteristics but also on the duration before these characteristics, such as phenotype, genotype, and niche, diverge. For characteristics like phenotype and genotype (or any other biological traits), new species will arise only if the differentiation time for both characteristics is sufficiently long (Liu, 2016) and the differentiation conditions, as defined in the following section, are satisfied.

When observed at different times, there may be one or multiple species within a population, as represented by:

$$\begin{cases} onespecies, t \le t_1 \\ onespecies, t_1 < t \le t_2 \\ twospecies, t > t_2. \end{cases} \quad (6)$$

Most species in nature are in a continuous process of differentiation. Complete reproductive, morphological, and niche isolations occur when divergence is fully realized (Liu, 2016). However, before reaching full speciation, species undergo further cycles of speciation. Species resulting from repeated splits of incomplete divergences exhibit incomplete reproductive isolation, frequent interspecific gene flow, and reticulate evolution (Liu, 2016). In defining species under these conditions, two points should be considered. First, it is unnecessary to satisfy all species concepts when defining a new species. Second, the isolation condition should be relaxed, not requiring strictly complete isolation (Liu, 2016). The complete isolation condition can be modified to the "degree of interspecific reproductive isolation is much greater than the degree of intraspecific reproductive isolation" or the "degree of interspecific morphological isolation is much greater than the degree of intraspecific morphological isolation". Specifically, this isolation can be characterized by the discontinuity of different dominant states and the variance among them after a period of differentiation.

To illustrate the potential differentiation outcomes for a new species, consider Figure 5, which shows the frequency distribution of dominant states within a population at a given point. Using phenotype differentiation as an example, initially, the global dominant phenotypes in the population arex_1 and x_2, respectively, owing to their highest fitness. Over time, these phenotypes differentiate into two new values of x_{11}, x_{12} and x_{21}, x_{22}, respectively, resulting in a bimodal frequency distribution, indicating that differentiation has occurred in one characteristic. Similarly, if another biological characteristic,

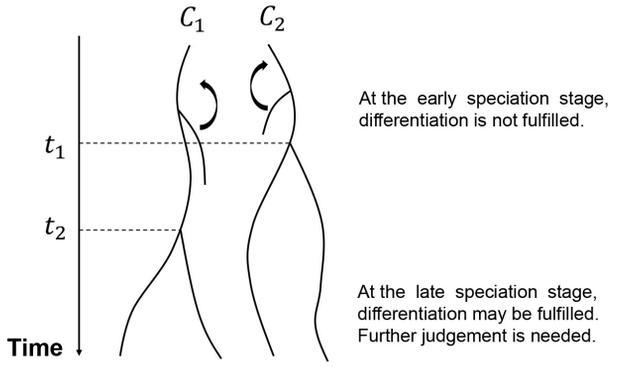

Figure 4 Schematic of species delimitation over time

Before reaching the late speciation stage, incomplete states undergo further cycles of speciation (arrows). Biological characteristic $C_1(C_2)$ differentiates at $t_1(t_2)$ after a relatively long time, allowing us to determine whether a species at different time points is a new species.

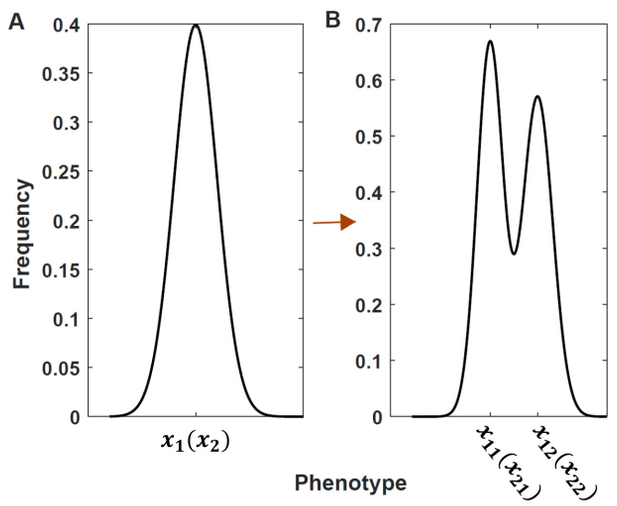

Figure 5 Frequency distribution of two phenotypes at different times

A: Frequency distribution curve of the state $x_1(x_2)$ during early differentiation. B: Frequency distribution curve of phenotype x_1 or x_2 at a specific moment after differentiation. Suppose that any two states x_1 and x_2 of original species A evolved under the influence of random mutation and drift, then different degrees of differentiation occur at the same or different times. Observing a "cutting plane" of species evolution reveals that $x_1(x_2)$ differentiates into $x_{11}(x_{21})$ and $x_{12}(x_{22})$, and the evolution is path-dependent. If the differentiated phenotypes (and other characteristics, such as genotypes) satisfy certain statistical conditions, individuals with phenotypes x_{11}, x_{21} (x_{11}, x_{22} or x_{12}, x_{21} or x_{12}, x_{22}) may represent new species.

such as genotype, also differentiates, a new species may successfully form. Based on our definition, individuals with characteristics x_{11} and x_{21} (x_{11} and x_{22}, x_{12} and x_{21}, or x_{12} and x_{22}) may belong to the same species. Next, we express the conditions for this mathematical form, using phenotype as an example. It is important to note that similar conditions apply when discussing speciation from the perspective of any other biological characteristics.

The average phenotype x_0 of a population evolves along different paths and may or may not differentiate into distinct phenotypes. This implies that the fitness landscape at a certain time may have multiple equilibrium points. Assuming a multi-peak scenario and using a function with multiple equilibrium points to describe this fitness landscape (Frank, 2011), we get:

$$f(x) = \sum_{i=1}^{n} (2|0.1 + x_i|^2 + 1) N(x_i, \sigma^2) \tag{7}$$

The fitness landscape is stable when $f(x) = 0$ for any arbitrary x. If a population with an initial average phenotype has more than one stable point, species divergence occurs. The distance of any two average phenotypes can be denoted as d, representing the discontinuity between them. Let σ_k indicate the variance within each average phenotype. The condition to delimit species is given by:

$$\frac{d}{\sigma_k} > 1 \ (k = i, j) \tag{8}$$

where: $d = |x_i - x_j|$.

This condition indicates that the discontinuity of one variable between subpopulations is greater than the difference of variables within the population. Additionally, a similar level of discontinuity and continuity of another variable is required to satisfy the species concept. If another biological characteristic also meets this condition, the corresponding individuals are considered different species. The detailed method for species delimitation is given as follows.

Species definition

For the statistical analysis of two or more variables across at least two levels of biological characteristics, whether genetic, morphological, or ecological, between two populations, if the differentiation time of these variables is sufficiently long and the relationship between the discontinuity d between populations and variance σ_k of variables within the population satisfies the inequation (8), then the individuals with the corresponding variables belong to different species.

Situations for species delimitation

Using the above definition, let us analyze some examples. Assuming that the differentiation time is sufficiently long, we can analyze the distance conditions of two average phenotypes in two subpopulations, with three typical situations shown in Figure 6. In the first situation, the distance between the two average phenotypes in the two subpopulations is $d_1 = |x_1 - x_2| = |(-1) - 2| = 3$, and their variances are $\sigma_1 = 1, \sigma_2 = 1.2$, respectively. This indicates that the discontinuous difference in morphology between the subpopulations is significantly greater than the continuous difference in morphology within any subpopulation, as $d_1 > \sigma_1, d_1 > \sigma_2$. If at least one other phenotype or biological characteristic also satisfies the same conditions, individuals in these two subpopulations belong to different species. In the second situation, it may initially seem difficult to determine whether they are different species. However, according to the above formula, the distance between the two average phenotypes in the two subpopulations is $d_2 = |x_2 - x_3| = |2 - 6| = 4$, but their variances are $\sigma_2 = 1.2, \sigma_3 = 4$, respectively. As $d_2 = \sigma_3$, individuals in these two subpopulations still belong to the same species. In the third situation, the distance between the two average phenotypes in the two subpopulations is $d_3 = |x_3 - x_4| = |6 - 9| = 3$, and the variances of the phenotypes are $\sigma_3 = 4, \sigma_4 = 6$, respectively. As $d_3 < \sigma_3$ and $d_3 < \sigma_4$, individuals in these two subpopulations still belong to the same species.

DISCUSSION

Researchers have suggested that speciation is a continuous

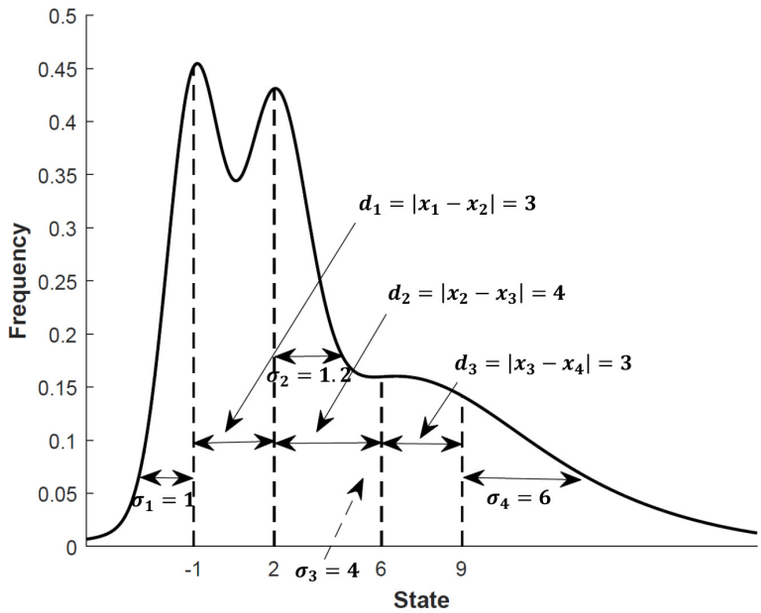

Figure 6 Different cases of phenotype differentiation

In the first situation, $d_1 = |x_1 - x_2| = |(-1) - 2| = 3, \sigma_1 = 1, \sigma_2 = 1.2, d_1 > \sigma_1$ and $d_1 > \sigma_2$. Individuals are considered different species if the same conditions hold when considering at least one other phenotypic value and characteristic. In the second situation, $d_2 = |x_2 - x_3| = |2 - 6| = 4, \sigma_2 = 1.2, \sigma_3 = 4, d_2 = \sigma_3$ and $d_2 > \sigma_2$. If these conditions are satisfied, then individuals are considered the same species regardless of other characteristics. In the third situation, $d_3 = |x_3 - x_4| = |6 - 9| = 3, \sigma_3 = 4, \sigma_4 = 6, d_3 < \sigma_3$ and $d_3 < \sigma_4$. If these conditions are satisfied, then individuals are considered the same species regardless of other characteristics.

process, and that the distribution of species characteristics varies across both time and geography (Darwin, 1859; Liu, 2016). Consequently, a fixed fitness expectation for a species may not be appropriate and analyzing species evolutionary trajectories may provide a more accurate description of speciation. Traditionally, evolutionary path theories have been interpreted considering a stationary fitness landscape (Frank, 2011). In such a scenario, Darwinian evolution, where phenotypes evolve toward higher fitness, is relatively straightforward to understand. Some researchers have focused on evolutionary paths by assuming constant trait fitness, concluding that natural selection favors the fastest route (Traulsen et al., 2007). However, fitness is influenced not only by population composition, including species interactions, but also be fluctuating environmental conditions, leading to changing fitness. This dynamic serves as the foundation for our investigation.

Various scholars studying population evolutionary dynamics have incorporated factors such as frequency, density, and environmental fluctuations into their models, including evolutionary games (Fudenberg et al., 2006; Huang & Traulsen, 2010; Huang et al., 2015; Willensdorfer & Nowak, 2005), ecological models (Doebeli & Hauert, 2005; Hauert et al., 2008), and eco-evolutionary models (Gokhale & Hauert, 2016; Govaert et al., 2019; Zhang & Hui, 2011). However, these studies have not explored the evolutionary trajectories from one trait to another, which is crucial for understanding speciation and the formation of the phylogenetic tree (Woese, 2000).

An average phenotype may therefore evolve into various nearby phenotypes with different probabilities at each time, based on the most recent fitness landscape influenced by species interactions and fluctuating environments. Over time, multiple paths with varying probabilities become possible. Many different trajectories can be chosen if environmental pressure is constrained; otherwise, there will be just one. Specifically, we can compute the transition probability from one state to another and display the distribution of traits at any given moment. These transitional phenomena align with biological realities, such as gene flow (Rieseberg & Burke, 2001; Van Alphen & Seehausen, 2001; Wang et al., 2020; Wu, 2001). In conclusion, discussing the evolutionary path that combines the dimensions of space and time makes sense. Within this framework, multiple trajectories can coexist with varying probabilities. The differentiation of species can be reflected by their frequency distribution during speciation. For example, if a species' initial frequency is 100%, and a new bimodal or multimodal frequency distribution emerges after several steps, this indicates the emergence of a new species.

Path-dependent evolution provides a new perspective on understanding speciation, particularly for species with lower fitness. Hybrids may also appear as original phenotypes move along these paths but are not considered as a new species due to gene backflow. Before reaching the final stage of speciation, interspecific gene flow may occur frequently, as postulated by Liu (2016). However, new hybrid species may form if genetic combinations, new genetic variations, and natural selection align with geographical distribution as they continue to evolve along these paths (Abbott et al., 2013). The emergence of a new species depends on the degree and number of differentiating traits, as well as the number of biological characteristics undergoing differentiation, rather than the time when the characteristics first diverge. If only one trait diverges, hybrids may result (Liu, 2016). Significantly, the earlier divergence begins, the more likely it is to form a new species (Liu, 2016).

For the mathematical formula of species definition, we focused on variations and discontinuities. As Hedberg noted, "when two populations display completely discontinuous variation in one character only (frequently supported by partial discontinuities in other characters) I have treated them as sub specifically distinct, whereas they are as a rule classified as

different species if discontinuous variation occurs in two or more independent features" (Hedberg, 1958). Despite criticisms of being oversimplified, this approach is still regarded as the most objective and operational species concept. Hong (2016) proposed a similar species concept, the morphobiological species concept. However, the number of characters used as the standard to define species is not the primary focus here. Instead, we focused on the conditions of speciation by considering two biological characteristics and the relationships among different average values for each biological characteristic.

CONCLUSIONS

In this work, we examine speciation based on evolutionary paths within the context of a changing fitness landscape. This approach offers a fresh understanding of how trait evolution is path-dependent. From this perspective, we also establish the conditions of speciation. Specifically, we propose that the selection of a trait depends not only on its fitness at a given time but also on the evolutionary paths it follows. These paths, measured by transition probabilities, are described mathematically (Li et al., 2023). While the evolutionary response to a novel environment ultimately results in changes in gene frequency, it is important to consider that other biological characteristics, such as phenotype, can also be used to delimit species by tracing their evolutionary history (Wilkins, 2006). Therefore, we focused on these two biological characteristics in the present study.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

L.M.L. performed the analyses and wrote the first draft of the manuscript. C. W. and W.R.W. provided the core idea and guidance of this work and edited the manuscript. All authors read and approved the final version of the manuscript.

REFERENCES

Abbott R, Albach D, Ansell S, et al. 2013. Hybridization and speciation. *Journal of Evolutionary Biology*, **26**(2): 229–246.

Arthur WB. 1989. Competing technologies, increasing returns, and lock-in by historical events. *The Economic Journal*, **99**(394): 116–131.

Bock WJ. 2004. Species: the concept, category and taxon. *Journal of Zoological Systematics and Evolutionary Research*, **42**(3): 178–190.

Claussen JC, Traulsen A. 2008. Cyclic dominance and biodiversity in well-mixed populations. *Physical Review Letters*, **100**(5): 058104.

Coyne JA, Barton NH, Turelli M. 1997. Perspective: a critique of Sewall Wright's shifting balance theory of evolution. *Evolution*, **51**(3): 643–671.

Cronquist A. 1978. Once again, what is a species?. *In*: Knutson L. Biosystematics in Agriculture. Montclair: Alleheld Osmun, 3–20.

Darwin CR. 1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. London: John Murray, 502.

De Queiroz K. 2007. Species concepts and species delimitation. *Systematic Biology*, **56**(6): 879–886.

Doebeli M, Hauert C. 2005. Models of cooperation based on the Prisoner's dilemma and the snowdrift game. *Ecology Letters*, **8**(7): 748–766.

Eldredge N, Cracraft J. 1980. Phylogenetic Patterns and the Evolutionary Process. New York: Columbia University Press, 103–104.

Frank SA. 2011. Natural selection. II. Developmental variability and evolutionary rate. *Journal of Evolutionary Biology*, **24**(11): 2310–2320.

Frauenfelder H, Leeson DT. 1998. The energy landscape in non-biological and biological molecules. *Nature Structural Biology*, **5**(9): 757–759.

Fudenberg D, Nowak MA, Taylor C, et al. 2006. Evolutionary game dynamics in finite populations with strong selection and weak mutation. *Theoretical Population Biology*, **70**(3): 352–363.

Gokhale CS, Hauert C. 2016. Eco-evolutionary dynamics of social dilemmas. *Theoretical Population Biology*, **111**: 28–42.

Gould SJ. 1977. Ontogeny and Phylogeny. Cambridge: Harvard University Press.

Govaert L, Fronhofer EA, Lion S, et al. 2019. Eco-evolutionary feedbacks —Theoretical models and perspectives. *Functional Ecology*, **33**(1): 13–30.

Hauert C, Wakano JY, Doebeli M. 2008. Ecological public goods games: cooperation and bifurcation. *Theoretical Population Biology*, **73**(2): 257–263.

Hedberg O. 1958. The taxonomic treatment of vicarious taxa. *Uppsala Universitets Å rsskrift*, **6**: 186–195.

Hong DY. 2016. Biodiversity pursuits need a scientific and operative species concept. *Biodiversity Science*, **24**(9): 979–999.

Huang WN, Hauert C, Traulsen A. 2015. Stochastic game dynamics under demographic fluctuations. *Proceedings of the National Academy of Sciences of the United States of America*, **112**(29): 9064–9069.

Huang WN, Traulsen A. 2010. Fixation probabilities of random mutants under frequency dependent selection. *Journal of Theoretical Biology*, **263**(2): 262–268.

Li ML, An K, Liu C, et al. 2023. The path integral formula for the stochastic evolutionary game dynamics. *Europhysics Letters*, **142**(6): 62001.

Liu JQ. 2016. "The integrative species concept" and "species on the speciation way". *Biodiversity Science*, **24**(9): 1004–1008.

Mallet J. 1995. A species definition for the modern synthesis. *Trends in Ecology & Evolution*, **10**(7): 294–299.

Mayden RL. 1997. A hierarchy of species concepts: the denouement in the saga of the species problem. *In*: Claridge MF, Dawah HA, Wilson MR. Species: The Units of Biodiversity. London: Chapman & Hall, 381–424.

Mayr E. 1942. Systematics and the Origin of Species from the Viewpoint of A Zoologist. New York: Columbia University Press.

Nowak MA. 2006. Evolutionary Dynamics: Exploring the Equations of Life. Cambridge: Harvard University Press.

Nowak MA, Sigmund K. 2004. Evolutionary dynamics of biological games. *Science*, **303**(5659): 793–799.

Rieseberg LH, Burke JM. 2001. A genic view of species integration. *Journal of Evolutionary Biology*, **14**(6): 883–886.

Schwilk DW, Ackerly DD. 2005. Limiting similarity and functional diversity along environmental gradients. *Ecology Letters*, **8**(3): 272–281.

Sherrington D. 1996. Landscape paradigms in physics and biology: Introduction and overview. *Physica D: Nonlinear Phenomena*, **107**(2-4): 117–121.

Smith JM. 1982. Evolution and the Theory of Games. Cambridge: Cambridge University Press, 10–27.

Steinberg B, Ostermeier M. 2016. Environmental Changes Bridge Evolutionary Valleys. *Science Advances*, **2**(1): e1500921.

Traulsen A, Iwasa Y, Nowak MA. 2007. The fastest evolutionary trajectory. *Journal of Theoretical Biology*, **249**(3): 617–623.

Van Alphen JJM, Seehausen O. 2001. Sexual selection, reproductive isolation and the genic view of speciation. *Journal of Evolutionary Biology*, **14**(6): 874–875.

Van Valen L. 1976. Ecological species, multispecies, and oaks. *Taxon*, **25**(2-3): 233–239.

Wang C, Li ML, Wang RW. 2022. Path probability selection in nature and path integral. *Scientific Reports*, **12**: 19044.

Wang J. 2015. Landscape and flux theory of non-equilibrium dynamical

systems with application to biology. *Advances in Physics*, **64**(1): 1–137.
Wang RW. 2021. The end of rationality and selfness —A story on the asymmetry, uncertainty and evolution of cooperation, Beijing: China Commerce and Trade Press.
Wang XF, He ZW, Shi SH, et al. 2020. Genes and speciation: is it time to abandon the biological species concept?. *National Science Review*, **7**(8): 1387–1397.
Whitlock MC, Phillips PC, Moore FBG, et al. 1995. Multiple fitness peaks and epistasis. *Annual Review of Ecology, Evolution, and Systematics*, **26**: 601–629.
Wiley EO. 1978. The evolutionary species concept reconsidered. *Systematic Biology*, **27**(1): 17–26.
Wilkins J. 2006. Species, kinds, and evolution. *Reports of the National Center for Science Education*, **26**(4): 36–45.
Willensdorfer M, Nowak MA. 2005. Mutation in evolutionary games can increase average fitness at equilibrium. *Journal of Theoretical Biology*, **237**(4): 355–362.
Woese CR. 2000. Interpreting the universal phylogenetic tree. *Proceedings of the National Academy of Sciences of the United States of America*, **97**(15): 8392–8396.
Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Sixth International Congress on Genetics*, **1**(6): 356–366.
Wright S. 1969. Evolution and the Genetics of Populations. New York: University of Chicago Press.
Wu CI. 2001. The genic view of the process of speciation. *Journal of Evolutionary Biology*, **14**(6): 851–865.
Wu CI, Wang XF, He ZW, et al. 2020. Replies to the commentaries on the question of 'Is it time to abandon the biological species concept?'. *National Science Review*, **7**(8): 1407–1409.
Zhang F, Hui C. 2011. Eco-evolutionary feedback and the invasion of cooperation in prisoner's dilemma games. *PLoS One*, **6**(11): e27523.