

Dynamics of Coexistence of Asexual and Sexual Reproduction in Adaptive Landscape

Shuyun Jiao^{*†}, Yanbo Wang[‡], Ping Ao^{*§}

^{*}Shanghai Center for Systems Biomedicine, Key Laboratory of Systems Biomedicine of Ministry of Education, Shanghai Jiao Tong University, 200240, Shanghai, P.R.China

[†]Department of Mathematics, Xinyang Normal University, 464000, Xinyang, Henan, P.R.China

[‡]Department of Computer Science and Engineering, Shanghai Jiao Tong University, 200240, Shanghai, P.R.China

[§]Department of Physics, Shanghai Jiao Tong University, 200240, Shanghai, P.R.China

Abstract—Background: The dynamics for species, especially rare species, with mixed type reproduction is instructive and meaningful for predicting the extinction of them. Though the extinction time is still a difficult problem for sexual or asexual populations. Adaptive landscape introduced by Wright, a powerful concept in systems biology can describe the evolution of organisms. To our knowledge, the dynamical of inhomogeneous reproductive organisms have not investigated by a simple model globally.

Methods: We describe how a Wright-Fisher process maps to the dynamics of a population with mixed type. We analytically construct adaptive landscape from the general diffusion equation. It shows that the construction is dynamical and the adaptive landscape is independent of the existence and normalization of the stationary distribution.

Results: We first give a global model describing the evolution of an inhomogeneous reproductive population by adaptive landscape. We visualize the dynamical behavior by adaptive landscape. Finite and infinite potential occur in the process. These results suggest a possible way to investigate the complex reproductive process in an inhomogeneous reproductive population.

Index Terms—Wright-Fisher Process, Adaptive Landscape, Stationary Distribution, Fixed Points

BACKGROUND

All organisms are under the action of mutation, selection and random drift and changing environment all the time. Their joint effects are complex. Especially the dynamical behavior of a population with mixed type of sexual and asexual reproduction is more complicated. There are some methods to explore the dynamics of a system. The prior and direct method is adaptive landscape. To build intuition, Wright introduced adaptive landscape [1], whose contours are meant to describe the net effects of these diverse population genetic forces. The appeal of this approach is its analogy to a physical landscape, whose gradient predicts a rolling marble's spatial trajectory [2]. Mathematically it is complex that required to fully integrate the genetics with Darwinian natural selection. Geometric representations of microevolutionary trajectories over adaptive landscape of one or another are motivated by the desire to provide some heuristic intuition into the process of microevolution. If we can extract the population genetics by investigating the contours of such a topographic surface, we can visualize how an evolving population will behave without always resorting to the algebraic heavy lifting. The system will

shift its configuration by following the steepest gradient on the potential function [2]. Though recently considerable progress [3] has been made on the evolutionary dynamics of transiting the fitness valley for finite populations in the presence of diverse evolutionary forces, there are also several others [2] [4] that have voiced the critique of adaptive landscape.

Evolutionary biologists have spent a lot of time attempting to identify factors that speed or slow adaptation. One of the most intensively studies of these factors is sexual vs. asexual reproduction [5]. For asexually reproducing population, without recombination, chromosomes are directly passed down to offsprings, as a consequence the deleterious mutations accumulate so that the fittest class loses. For sexually reproducing population, because of the existence of recombination between parental genomes, a parent carrying high mutational loads can have offspring with fewer deleterious mutations. The high cost of sexual reproduction is thus offset by the benefits of inhibiting the ratchet [6]. How about the coexistence and coevolution of sexuals and asexuals? It is significant for the evolutionary dynamics of mixed type population. Because the evolution for this kind of species such as rare species is meaningful. If we can distill the population genetics by exploring the contours of such a topological surface, we can visualize how the population will behave. Further we can make the possible prediction in the presence of diverse parameters by changing corresponding population genetic factors. Authors in [7] explored the coexistence and coevolution dynamics of sexual and asexual competitors. They focused on determining the condition when the advantage of sexuals will outway its three disadvantages. Authors in [8] explored the rates of accumulation of both beneficial and harmful mutations with weak selection depend on population variance of the number of mutant genes for hermaphroditic, selfing and asexual populations. We first consider the issue by adaptive landscape. This work can imply advantage of adaptive landscape by projecting the system into allele state space. In addition, we expect this work can contribute to clearing some controversies about the adaptive landscape.

The key concept in constructing adaptive landscape is of potential function as a scalar function. There is a long history of definition, interpretation, and generalization of potential. Potential has also been applied to biological systems in various

ways. The usefulness of a potential reemerges in the current study of dynamics of gene regulatory networks [9], such as its application in genetic switch [10][11][12]. The role of potential is the same as that of adaptive landscape. In this article, we do not distinct them.

In this article we present an approach to an inhomogenous genetic structure population with constant size, projecting evolutionary dynamics of the population with mixed type reproduction to one dimensional Wright-Fisher model where one locus with two alleles are used to depict all different types of individuals. Before sexual reproduction, the population is composed of haploid asexuals. After sexual reproduction, the population is composed of haploid and diploid individuals. We explore the dynamics in the presence of irreversible deleterious mutation, viability selection and random drift. These results suggest the dynamical behavior could be derived more quickly and more convenient by adaptive landscape. Additionally, we expect this work can contribute to clearing some controversies about the adaptive landscape.

METHODS

Model description

We consider here the mode of reproduction - coexistence of asexual and sexual reproduction. We aim to get the dynamical information for the inhomogenous genetic population in presence of irreversible mutation, selection and random drift. For asexuals, Muller ratchet is an important process. Muller's ratchet is the process by which genomes of a finite population composed of asexual individuals accumulate deleterious mutations in an irreversible manner [13][14]. For sexuals, with recombination, the process is like Muller ratchet under the same conditions. Consider a mixed type reproduction population of fixed size with discrete generations $t = 0, 1, 2, \dots$. The starting point in a generation is regarded as adult stage, new mutations occur at reproduction and all mutations are assumed to deleteriously affect viability but have no effect on fertility. After all selection has occurred and immediately prior to reproduction. Supposed population size is always fixed each generation by ecological thinning, then there are always alleles with constant number in the gene pool. Here we consider one locus with two alleles A and B , that is, initially there are two classes in the haploid population, one class with allele A while the other with allele a . Among them αN alleles reproduce asexually. $(1 - \alpha)N$ alleles reproduce sexually. Sexuals can reproduce asexually at fixed probability β . So there are $\alpha N + (1 - \beta)(1 - \alpha)N$ alleles reproduce asexually. Sexuals are composed of individuals with genotypes AB and BB . Supposed mutation from allele A to B is deleterious, we assume population of constant size $N > 1$, generations are non-overlapping, the generation length for asexual and sexual reproduction is same. The lifecycle of the individuals in the population is from adults to juveniles, during which we consider the change of allele A in the presence of irreversible mutations, selection and random genetic drift. Given above assumptions, we can study the evolution of allele A . The frequency of allele A in generation t is x_t while

that of allele B is $1 - x_t$. Let μ be the probability that an offspring of an adult with allele A is an individual with allele B . It is labeled by $M_{1,0}$, that is, $M_{1,0} = \mu$. Analogously, $M_{0,0} = 1 - \mu$, $M_{0,1} = 0$, $M_{1,1} = 1$. The relative viability of individuals with allele A and AB is $\nu = 1$ while that of individuals with allele B and BB is $\nu_1 = 1 - \sigma$, where σ can be treated as effective selection rates associated with deleterious mutations. Then in generation $t + 1$, after selection and deleterious mutation the frequency of allele A is $(1 - \mu)x_t$, the frequency of allele B with asexual reproduction in two generations is $(1 - \sigma)(\alpha + (1 - \beta)(1 - \alpha))(1 - x_t)$, the frequency of allele B with sexual reproduction in the form of AB is $(1 - x_t)\beta(1 - \alpha)(1 - \mu)$, the frequency of allele B with sexual reproduction in the form of BB is $(1 - x_t)\beta(1 - \alpha)(1 - \sigma)$. So the frequency of allele A in the whole population is

$$x_{t+1} = \frac{(1 - \mu)x_t / (x_t(1 - \sigma\mu) + (1 - x_t)[(1 - \sigma)(1 - \alpha\beta - \beta) + \beta(1 - \alpha)(2 - \sigma - \mu)])}{(1 - \alpha\beta - \beta) + \beta(1 - \alpha)(2 - \sigma - \mu)}. \quad (1)$$

Under the general diffusion approximation, frequency x_t is treated as continuous quantities x , and this also leads to the distribution of the frequency of allele A being probability density. Let $\rho(x, t)$ be the probability density of the frequency of allele A being x at time t . The diffusion equation obeys the following formula [15] [16]

$$\partial_t \rho(x, t) = \partial_x^2 [V(x)\rho(x, t)/2] - \partial_x [M(x)\rho(x, t)], \quad (2)$$

with

$$M(x) = \frac{(1 - \mu)x / (x(1 - \sigma\mu) + (1 - x)[(1 - \sigma)(1 - \alpha\beta - \beta) + \beta(1 - \alpha)(2 - \sigma - \mu)])}{(1 - \alpha\beta - \beta) + \beta(1 - \alpha)(2 - \sigma - \mu)} - x, \quad (3)$$

and

$$V(x) = \frac{x(1 - x)}{N}, \quad (4)$$

where $M(x)$ represents the average transition rate of x or driving force [15][17] and $V(x)$ is the corresponding variance.

Adaptive landscape

We can also depict the same evolutionary process by the following symmetric equation

$$\partial_t \rho(x, t) = \partial_x [\epsilon D(x) \partial_x - f(x)] \rho(x, t) \quad (5)$$

with

$$f(x) = \frac{(1 - \mu)x / (x(1 - \sigma\mu) + (1 - x)[(1 - \sigma)(1 - \alpha\beta - \beta) + \beta(1 - \alpha)(2 - \sigma - \mu)])}{(1 - \alpha\beta - \beta) + \beta(1 - \alpha)(2 - \sigma - \mu)} - x - \frac{(1 - 2x)}{2N}, \quad (6)$$

$$\epsilon D(x) = \frac{x(1 - x)}{2N}. \quad (7)$$

Adaptive landscape is directly given under natural boundary condition as

$$\Phi(x) = \int \frac{f(x)}{D(x)} dx. \quad (8)$$

We are interested in the dynamical property of adaptive landscape, so we treat Φ and Φ/ϵ no difference in this respect, that is, for convenience we can take $\epsilon = 1$ of $\epsilon D(x)$. Then

$$\begin{aligned}\Phi(x) &= \int \frac{f(x)}{\epsilon D(x)} dx \\ &= \frac{2N\mu(1-\sigma)}{1-\sigma\mu} \ln(1-x) - \ln x(1-x) \\ &\quad + \frac{2N(1-\mu)}{1-\sigma\mu} \ln(x(\sigma - \sigma\mu - \beta(1-\mu) \\ &\quad - \alpha(3-2\sigma-\mu))) + 1 - \sigma \\ &\quad + \beta(1-\mu - \alpha(3-2\sigma-\mu)).\end{aligned}\quad (9)$$

Here the adaptive landscape is composed of three terms. The first term and the third term quantify the effect of irreversible mutation and selection respectively, the second term quantifies the effect of random drift. When the parameter $\beta = 1$ or $\alpha = 1, \beta = 0$, the genetic structure of the population turns to the homogenous genetic structure- population composed of asexual individuals. When the parameter $\alpha = 0, \beta = 0$, the genetic structure of the population turns to another case of homogenous genetic structure- population composed of sexual individuals.

In addition, the symmetric Eq.(5) has two advantages. On the one hand, the adaptive landscape is directly read out when the detailed balance is satisfied. On the other hand, the constructive method is dynamical, independent of existence and normalization of stationary distribution. We call $f(x)$ directional transition rate, integrating the effects of $M(x)$ and the derivative of $V(x)$. Directional transition rate can give equilibrium states when $f(x)$ is in linear form.

Under natural boundary condition satisfying that the probability flux of the system at boundary is zero, and the probability flows in $[0, 1]$. The stationary distribution is given by

$$\rho(x, t = +\infty) = \frac{1}{Z} \exp\left(\frac{\Phi(x)}{\epsilon}\right).$$

Stationary distribution can also be expressed as

$$\begin{aligned}\rho(x, t = +\infty) &\propto \exp\left(\frac{2N\mu(1-\sigma)}{1-\sigma\mu} \ln(1-x) - \ln x(1-x)\right) \\ &\quad + \frac{2N(1-\mu)}{1-\sigma\mu} \ln(x(\sigma - \sigma\mu - \beta(1-\mu) \\ &\quad - \alpha(3-2\sigma-\mu))) + 1 - \sigma \\ &\quad + \beta(1-\mu - \alpha(3-2\sigma-\mu))).\end{aligned}$$

It has the form of Boltzmann-Gibbs distribution [18], so the scalar function $\Phi(x)$ naturally acquires the meaning of potential energy [9]. The value of Z determines the normalization of $\rho(x, t = +\infty)$ in terms of probability, and the finite value of Z manifests the normalization of $\rho(x, t = +\infty)$. If $Z = +\infty$, the actual stationary distribution is not $\rho(x, t = +\infty)$, this demonstrates the absorbing phenomena occur. Combining $\rho(x, t = +\infty)$ at boundary, the stationary distribution can be actual stationary distribution. The constant ϵ holds the same

position as temperature of Boltzmann-Gibbs distribution in statistical mechanics. The constant "temperature" does not hold the nature of temperature in Boltzmann-Gibbs distribution.

RESULTS AND DISCUSSION

Previous works mainly focus on the coexistence of sexual and asexual in a population. Recently there is a work about the competition advantage of two different percentage of asexuals in mixed type of sexual and asexual populations [19]. Authors in [20] use the method of game theory to indicate the dynamics of a mixed type population. Their method in [20] has the advantage in the presence of inconsistency of cycles for sexual and asexual reproduction. But the interaction between the two modes of reproduction is not evident. Here we model the dynamics at the allele level. We analyze the evolutionary process in all parameter regimes based on Fokker-Planck equation by adaptive landscape. We investigate the dynamics by discussing the positions of the fixed points and boundary points $x = 0, 1$. We address the condition of finite and infinite potential occurring analytically.

Regimes of parameters α, β

To understand the population dynamics with a mixed type of sexual and asexual reproduction, a full characterization of dynamical process is prerequisite. Here we study it in the framework of adaptive landscape in detail.

Let

$$\Phi'(x) = 0, \quad (11)$$

that is

$$\begin{aligned}2(N-1)(\sigma - \sigma\mu - C)x^2 - (2-3\sigma + 2N\sigma + \sigma\mu \\ - 2N\mu - (2N-3)C)x + 1 - \sigma + C = 0.\end{aligned}\quad (12)$$

Where

$$C = \beta(1-\mu - \alpha(3-2\sigma-\mu)). \quad (13)$$

It is a quadratic equation regard to x . Then we can get the fixed points.

They are

$$x_{1,2} = \frac{2-2N\mu - (2N-3)C - 3\sigma + 2N\sigma + \sigma\mu \pm D}{4(N-1)(\sigma - \sigma\mu - C)}, \quad (14)$$

where

$$\begin{aligned}(10)D &= (-8(N-1)(1+C-\sigma)(\sigma - \sigma\mu - C) \\ &\quad + (-2 + 2N\mu + (2N-3)C + 3\sigma - 2N\mu - \sigma\mu)^2)^{1/2}.\end{aligned}\quad (15)$$

From the expression of adaptive landscape $\Phi(x)$, we may find there are two singular points 0 and 1 of adaptive landscape, characterized by infinity values. And there is a point x^* in the third term of adaptive landscape. Where

$$x^* = -\frac{1-\sigma + \beta(1-\mu - \alpha(3-2\sigma-\mu))}{\sigma - \sigma\mu - \beta(1-\mu - \alpha(3-2\sigma-\mu))}. \quad (16)$$

It may be singular, may not be. Here we study the dynamical behaviors by investigating the position and adaptiveness of all fixed points and singular points. Possible proportion of asexuals and possible probability of sexuals is demonstrated in Fig. 1.

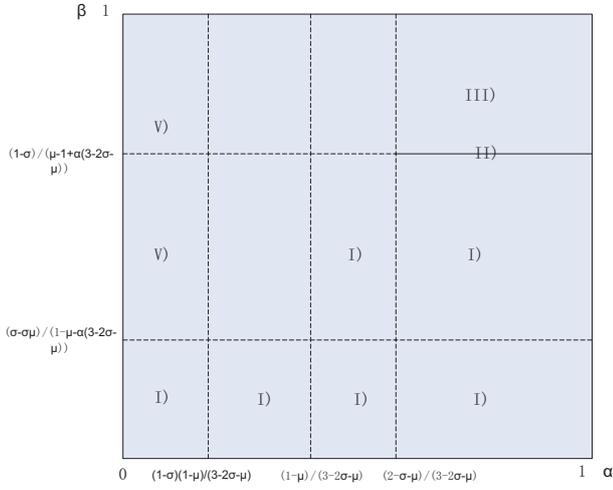


Fig. 1. Relation between adaptive landscape and parameters α and β . There are two singular points with $x = 0$ and $x = 1$ in the regions of I, II) and V). There are three singular points with $x = 0$, $x = 1$ and $x = x^*$ in the region III). The regions with no words can not be reached. Solid line implies the corresponding regime included, dashed line implies the corresponding regime removed.

Irreversible mutation, selection and random drift balance

We further get the parameters regions for all possible cases. In the following we give the details of the parameters regimes according to the different kinds of potential in the presence of two stable states. First we denote

$$\beta_1 = \frac{-(2-6N\mu+4N^2\mu-\sigma+4N\sigma-4N^2\sigma-\sigma\mu+2N\mu\sigma)}{(2N-1)^2(1-\mu-\alpha(3-2\sigma-\mu))} - \frac{4\sqrt{N(N-1)(1-\mu)(2N\mu-1+\sigma\mu-2N\sigma\mu)}}{(2N-1)^2(1-\mu-\alpha(3-2\sigma-\mu))}, \quad (17)$$

$$\beta_2 = \frac{-(2-6N\mu+4N^2\mu-\sigma+4N\sigma-4N^2\sigma-\sigma\mu+2N\mu\sigma)}{(2N-1)^2(1-\mu-\alpha(3-2\sigma-\mu))} + \frac{4\sqrt{N(N-1)(1-\mu)(2N\mu-1+\sigma\mu-2N\sigma\mu)}}{(2N-1)^2(1-\mu-\alpha(3-2\sigma-\mu))}. \quad (18)$$

I) Finite potential

i) Finite potential in the absence of two stable states

Under the parameters regimes $1 > \alpha > (1-\mu)/(3-2\sigma-\mu)$, $\mu < \sigma < (2N\mu-1)/(2N\mu-\mu)$, $\beta = (1-\sigma)/(\alpha(3-2\sigma-\mu)+\mu-1)$, there are two unstable states with allele $x = 0$, $x = 1$ and one stable states with allele $x = x_2$ in the system. The shape of potential is like a inverse V-shape. The population tends to evolve as a mixed type with sexuals and asexuals.

ii) Finite potential in the presence of two stable states

Under the parameters regimes $1 > \alpha > (1-\mu)/(3-2\sigma-\mu)$, $\mu < \sigma < (2N\mu-1)/(2N\mu-\mu)$, $\beta < \min(1-\sigma)/(\alpha(3-2\sigma-\mu)+\mu-1)$, $-\beta_2$, and regimes $1 > \alpha > (1-\mu)/(3-2\sigma-\mu)$, $\mu < \sigma < (2N\mu-1)/(2N\mu-\mu)$, $\beta > -\beta_1$, and regimes $0 < \alpha < (1-$

$\mu)/(3-2\sigma-\mu)$, $\mu < \sigma < (2N\mu-1)/(2N\mu-\mu)$, $\beta < \min(\sigma-\sigma\mu)/(1-\mu\alpha(3-2\sigma-\mu))$, β_1 , and regimes $0 < \alpha < (1-\mu)/(3-2\sigma-\mu)$, $\mu < \sigma < (2N\mu-1)/(2N\mu-\mu)$, $\beta > \beta_2$, corresponding to the case $1 > x_2 > x_1 > 0 > x^*$, there are two unstable states with allele $x = x_1$, $x = 1$ and two stable states with allele x_0 , $x = x_2$ in the system. The population with allele greater than $x = x_1$ tends to evolve to the state with allele $x = x_2$ as a mixed type with sexuals and asexuals. The population with allele less than $x = x_1$ tends to evolve as a homogenous genetic population only with allele B . Ultimately the population with high possibility goes to state with allele $x = 0$.

II) Infinite potential

i) Infinite potential in the absence of two stable states

In the cases such as $x_2 = 1 > x^* > 0 > x_1$, $1 > x_2 = x^* > 0 > x_1$, $x^* > 1 = x_2 > 0 > x_1$, $x^* > x_2 > 1 > 0 > x_1$, $x^* = x_2 > 1 > 0 > x_1$, $x_2 > 1 > 0 = x^* = x_1$, $x_2 = 1 > 0 = x^* = x_1$, $1 > x_2 = 0 = x^* > x_1$, $x_2 > 1 = x_1 > 0 > x^*$, $x_2 > x_1 > 1 > 0 > x^*$, $x_2 = 1 > x_1 > 0 > x^*$, $x_1 = x_2 > 1 > 0 > x^*$, $x_1 = x_2 = 1 > 0 > x^*$, $1 > x_1 = x_2 > 0 > x^*$, $0 > x_1 = x_2$ and $0 > x^*$, $0 > x_2 > x_1$ and $0 > x^*$, there is only one stable state with allele $x = 0$ in the system. The population tends to evolve to the state composed of allele B . Ultimately the population is composed of individuals with allele B .

ii) Infinite potential in the presence of two stable states

With the three cases such as $x_2 > 1 > x_1 > 0 > x^*$, corresponding to parameters regimes $1 > \sigma > (2N\mu-1)/(2N\mu-\mu)$, $1 > \alpha > (1-\mu)/(3-2\sigma-\mu)$, $0 < \beta < (1-\sigma)/(\alpha(3-2\sigma-\mu)+\mu-1)$ and regimes $\sigma > (2N\mu-1)/(2N\mu-\mu)$, $0 < \alpha < (1-\mu)/(3-2\sigma-\mu)$, $1 < \beta < (\sigma-\sigma\mu)/(1-\mu-\alpha(3-2\sigma-\mu))$, cases $x_2 > 1 > x^* > 0 > x_1$, corresponding to parameters regimes $1 > \sigma > (2N\mu-1)/(2N\mu-\mu)$, $1 > \alpha > (1-\mu)/(3-2\sigma-\mu)$, $1 > \beta > (1-\sigma)/(\alpha(3-2\sigma-\mu)+\mu-1)$, and $x^* > 1 > x_2 > 0 > x_1$, corresponding to parameters regimes $\sigma > (2N\mu-1)/(2N\mu-\mu)$, $1 > \alpha > (1-\mu)/(3-2\sigma-\mu)$, $\beta < (1-\sigma)/(\alpha(3-2\sigma-\mu)+\mu-1)$ and regimes $1 > \sigma > (2N\mu-1)/(2N\mu-\mu)$, $0 < \alpha < (1-\mu)/(3-2\sigma-\mu)$, $1 > \beta > (\sigma-\sigma\mu)/(1-\mu-\alpha(3-2\sigma-\mu))$, there are two stable states with allele $x = 0$, $x = 1$ and an unstable states in the system. The population evolves to which stable states is decided by the initial states. If the initial states with allele locates the attraction of the state with allele $x = 0$.

All kinds of shapes for adaptive landscape are inverse V-shape, S-shape rotated 90 degrees, L-shape and U-shape.

Discussion

The present article presents a new approach to explore the dynamics of populations with mixed type reproduction. Inspired by a recent work [21], we connect it to one locus Wright-Fisher model with mixed type reproduction, the allele pool is composed of N alleles. Direct classical diffusion approximation of Wright-Fisher model can reduce complex calculation to solve matrix equations, this method is functional

especially when the dimension of the matrix is higher. Our theoretical results makes the application of the method proposed in [22] in the system of mixed type with sexual and asexual reproduction come true. Our method demonstrate the method can describe the global dynamical behavior, and does not need the existence and normalization of stationary distribution. Our dynamical constructive method is independent of the stationary distribution.

The previous work [20] used the method of game theory to indicate the dynamics of a mixed type population. Their method has the advantage in the presence of inconsistency of cycles for sexual and asexual reproduction. But the interaction between the two modes is not evident. Compared with it, we model the dynamics at the allele level. We analyze the evolutionary process in all parameter regimes based on Fokker-Planck equation by adaptive landscape. Our method investigates the global dynamical property of the system more directly than theirs, though our model is limited at the same length of reproductive cycle for sexual and asexual reproduction. In addition, our results demonstrate the condition under which the two finite and infinite potentials occur. Recently there is another work about the competition advantage of two different percentage of asexuals in mixed type of sexual and asexual populations [19], though they focus on a different issue. In the future, we consider the proportion of asexuals in a population affect the dynamical behavior, especially the transition between two stable states.

To summarize, we first explore the dynamics of population evolution with mixed type reproduction by adaptive landscape globally and theoretically. In this framework the conditions of different dynamical behaviors are investigated. Especially finite and infinite potential occur. Hence it allows us a new way to get the dynamics of a mixed type reproduction. In this perspective our work may be a starting point for comparison the advantage of different modes of reproduction and exploring the dynamics and extinction for populations with mixed type reproduction in more general situations.

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