Landscape construction in non-gradient dynamics: A case from evolution

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The adaptive landscape, an energy-like concept, lies in the interdiscipline between the evolution theory and the nonequilibrium theory. It was first proposed by Wright to illustrate his evolution theory, but its existence for non-gradient dynamics is greatly controversial. Following a quantitative framework which is consistent with Wright’s theory, we construct the adaptive landscape for a typical 2-d non-gradient deterministic evolution model, where the adaptive landscape was thought not to exist. Our results show that the population moves along the path with increasing adaptiveness, but not necessarily following the steepest gradient path, which demonstrates that the gradient criterion is irrelevant to the existence of the adaptive landscape. Thus, our results clarify the long confusion in the community.

Keywords: non-gradient system, adaptive landscape, linkage disequilibrium, evolution theory

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1. Introduction

The adaptive landscape was first proposed by Wright\cite{1}, one of the pioneers in population genetics, to illustrate his evolution theory. This notion has also been used as a metaphor as well as a quantification tool in branches of modern biology\cite{2-13} and in nonequilibrium physics\cite{14-20}, and in principle it may be identified in other dynamical problems\cite{21-23}. Wright’s verbal theory is quantified by a novel dynamical framework\cite{9,16}, supported by the real application for a genetic switch system\cite{12}, by the physical experiment\cite{24}, and later by other proposed theories\cite{17,25,26}. Consistent with Wright’s theory, the framework theoretically incorporates the adaptive landscape into the decomposition of the dynamics, but the practical construction generally remains difficult, which leads to the great confusion\cite{27-29} about the existence of the adaptive landscape for the non-gradient dynamics.

Wright’s theory is summarized in the textbook\cite{30} as: the population approaches the local peak “in conformity with the ‘increase in mean fitness’ concept”, and it can shift to other peaks by the influence of the random factors. Both the verbal theory and the quantitative framework provide generally a stochastic characterization about the evolution, while the deterministic dynamics ($\dot{q} = f(q)$) is the limit case where the strength of the noise is zero. In the deterministic systems, the non-decreasing of the adaptiveness is mathematically captured by the Lyapunov property from engineering\cite{31,32}. In fact, the function with the Lyapunov property was originally proposed to characterize the local stability near equilibrium\cite{21,31,32}, and it is generalized to be the global concept during the quantification of the adaptive landscape\cite{9,16,33}.

The gradient criterion ($\nabla \times f(q) = 0$) equivalently refrains the corresponding system to be a gradient system ($\dot{q} = f(q) = \nabla \phi(q)$). It is straightforward to construct the adaptive landscape by integration in a system satisfying the gradient criterion, but the gradient criterion is overly taken for granted as the general existence criterion\cite{29}. Meanwhile, the landscape is considered not to exist for the general non-gradient dynamics\cite{27,28}.

In a well posed 2-d non-gradient deterministic evolution model\cite{29}, we demonstrate that the gradient criterion is irrelevant to the existence of the adaptive landscape, and the adaptive landscape can coexist with non-gradient dynamics.
We construct the adaptive landscape either analytically or numerically in typical parameter regions for this model. After the construction, we decompose the dynamics into two components: the dissipative part driving the population to the local peak, and the conservative part driving the population moving on the equi-potential surface of the adaptive landscape. Our results show that the conservative part is not zero in current model, which is vertical to the gradient of the adaptive landscape. With the conservative part, the population deviates from the gradient path, which generally breaks the gradient criterion.

We introduce the framework and the decomposition for deterministic dynamics in the section 2. In the section 3, we list the details about the model where the adaptive landscape was thought not to exist. We put our constructions for this model with three typical sets of parameters in section 4. At last, we discuss our results in section 5.

2. Framework

In a deterministic model, the evolution is described by

$$\dot{q} = f(q)$$

(1)

where $q$ is generally a n dimension vector of system variables, $\dot{q}$ denotes its time derivative, $f$ represents all (deterministic) evolutionary forces in the system. In the framework$^{[9,16]}$, an explicit decomposition of $f$ into three dynamical components has been proposed as

$$f(q) = [D(q) + Q(q)] \cdot \nabla \phi(q),$$

(2)

where $\phi(q)$ is the adaptive landscape, $D(q)$ is the diffusion matrix (symmetric and semi-positive definite), and $Q(q)$ is an anti-symmetric matrix.

With the decomposition, the dynamics can be separated into two parts: the dissipative part $f_d(q) = D(q)\nabla \phi(q)$ which contributes to the increase of the adaptiveness; the conservative part $f_c(q) = Q(q)\nabla \phi(q)$ which does not change the adaptiveness. The structure of the decomposition guarantees the the Lyapunov property of the adaptive landscape:

$$\dot{\phi}(q(t)) \geq 0,$$

(3)

which manifests Wright’s idea that a population’s evolution can be visualized as the “adaptive” movements on a landscape. A population always heads for higher adaptiveness (when
\( \dot{\phi}(q(t)) > 0 \) or conserves its adaptiveness at specific states (when \( \dot{\phi}(q(t)) = 0 \)), providing a global characterization about the long-term evolution. Multiply \( \nabla \phi(q) \) to both sides of Eq. 2 the term \( Q \) is eliminated because it is anti-symmetric, and we get the static Hamilton-Jacobi equation

\[
[\nabla \phi(q)]^\top \cdot f(q) - [\nabla \phi(q)]^\top \cdot D(q) \cdot \nabla \phi(q) = 0. \tag{4}
\]

We put the mathematical details in Appendix A.

It is worth noting that the adaptive landscape may be not unique for general deterministic dynamics (shown by our Eq. 2 and Eq. 4). For example, we multiply any positive number to to the adaptive landscape \( \phi(q) \), and divide it from \( D(q) \) and \( Q(q) \) at the same time, which will leaves Eq. 2 and Eq. 4 still valid. Bearing in mind our motivation to clarify the existence issue of the adaptive landscape for non-gradient dynamics in current paper, we note that this feature does not undermine our construction. Therefore, we treat the \( D(q) \) and \( Q(q) \) as degrees of freedom for our constructions in current paper. The two factors should be fully determined after introducing the constraints from the stochastic part, which has been discussed in previous works\[9,16\].

In this paper, we find the Lyapunov function \( \phi(q) \) for the deterministic model, capturing the non-decrease of the adaptiveness. The other dynamical factors \( D(q) \) and \( Q(q) \) are constructed as\[33\]

\[
D = \frac{f \cdot \nabla \phi}{\nabla \phi \cdot \nabla \phi} \cdot I, \tag{5}
\]

\[
Q = \frac{f \times \nabla \phi}{\nabla \phi \cdot \nabla \phi}. \tag{6}
\]

where \( I \) is the identity matrix. The cross product of two vectors \( x, y \in R^n \) is an anti-symmetric matrix in \( R^{n \times n} \) defined as \( (x \times y)_{i,j} = (x_i y_j - x_j y_i) \). They are consistent with the Eq. 2 to Eq. 4 proved in the work\[33\].

3. Model

The model\[29\] describes a population’s evolution on two loci: the \( A/a \) pair and \( B/b \) pair, about its change of the frequencies of the genotypes \( p_{AB}, p_{Ab}, p_{aB}, p_{ab} \). With additional simplifying constraints (selective symmetry on \( Ab \) and \( Ab \) leads to \( p_{Ab} = p_{ab} \) at all times),
the model is expressed in the allele frequency \((q_1 = p_A = p_B)\) VS linkage disequilibrium \((q_2 = p_{ab}p_{AB} - p_{AB}p_{aB})\) space \((\dot{q}_1 = f_1, \dot{q}_2 = f_2)\):

\[
\begin{align*}
    f_1(q) &= \frac{q_2[s_2 - s_1 - q_1(s_2 - 2s_1)] + (1 - q_1)q_1(s_2 - 2s_1 + s_1)}{1 + 2q_1s_1 + (q_2 + q_1^2)(s_2 - 2s_1)} \\
    f_2(q) &= \frac{(1 - r) \cdot \left\{ q_2(1 + s_2) - [2q_1q_2(1 - q_1) - q_2^2 - q_1^2(1 - q_1)^2](s_2 - 2s_1 - s_1^2) \right\}}{[1 + 2q_1s_1 + (q_2 + q_1^2)(s_2 - 2s_1)]^2} - q_2(7)
\end{align*}
\]

where \(s_1\) and \(s_2\) denotes the selective advantages of the genotype \(Ab/aB\) and the genotype \(AB\) over the genotype \(ab\), \(r\) is the recombination rate. The spatial-temporal (frequency and generation) continuity was assumed for convenient analysis of the deterministic dynamics of the model. We use the conventional physical notations in Eq. 7, and list the model with the original notations in Appendix B.

In the \(q_1 \times q_2\) space, the two variables \(q_1\) and \(q_2\) is confined in

\[
0 \leq q_1 \leq 1, \quad \text{Max}[-q_1^2, -(1 - q_1)^2] \leq q_2 \leq q_1(1 - q_1). \tag{8}
\]

The parameter region for the model is

\[
-1 < s_1 < s_2, \quad 0 < s_2, \quad 0 \leq r \leq \frac{1}{2}. \tag{9}
\]

The adaptive landscape was thought[29] not to exist for this model, because the gradient criterion \((\nabla \times f(q) = 0)\) is violated.

4. Constructions

We construct the adaptive landscape in three typical parameter regions[29], including biologically or mathematically important cases. In the first case where recombination vanishes \((r = 0)\), we bring in the mean fitness[34,35] defined for a 4-d model in Eq. 10 in order to construct the adaptive landscape. The two models can be connected by a nonlinear transformation, which preserves the Lyapunov property.

In the rest two cases, the whole parameter region are divided into two regions, according to their different dynamical behavior[29]: the second case \((0 \leq s_1 < s_2)\) is the single peak case where we find a direct construction of the landscape, which captures the global stability of
Figure 1: We construct the adaptive landscape as $\phi(q) = W(q)$, and we represent its value by the color in the figure. We plot the gradient field of the adaptive landscape, and we also plot one typical trajectory that deviates from the gradient, which generally breaks the gradient criterion. The parameters are $s_1 = 0.08$, $s_2 = 0.1$, and $r = 0$.

The dynamics, consistent with the local stability analysis[29]; in the third case, we construct the landscape numerically for a typical double peak case, where the landscape determines the attracting basins of the two peaks and the boundary of the basins.

**4.1. Case 1: Only selection ($r = 0$): single peak case**

In this case, only the selection drives the population to evolve. Label the genotypes $AB, Ab, aB, ab$ as $1, \ldots, 4$. Due to the selective symmetry, the 2-d model in Eq. 7 corresponds to the behavior of a 4-d model[34]

$$\dot{p}_i = \frac{w_i \cdot p_i}{W} - p_i \quad i = 1, \ldots, 4, \quad (10)$$

on the invariant surface $S = \{p_i \mid p_i \geq 0, \sum_i p_i = 1, p_2 = p_3; \}$ and $W$ is the mean fitness[34,35]

$$W = \sum_{i=1}^{4} w_i \cdot p_i \quad (11)$$

where $w_1 = 1 + s_2$, $w_2 = w_3 = 1 + s_1$, and $w_4 = 1$ (the parameter region for $s_1, s_2$ is in Eq. 9).
The one-to-one mapping between the 4-d model on the surface $S$ and the 2-d model in the region in Eq. 8 is

\[ q_1 = p_1 + p_2 \]
\[ q_2 = p_1 \cdot p_4 - p_2 \cdot p_3 \] (12)

and

\[ p_1 = q_1^2 + q_2 \]
\[ p_2 = p_3 = q_1 - q_1^2 - q_2 \]
\[ p_4 = 1 - 2q_1 + q_1^2 + q_2 \] (13)

The Lyapunov property is invariant under coordinate transformation (Appendix D), and the mean fitness $W$ in Eq. 11 has the Lyapunov property

\[ \dot{W} = \sum_i \dot{p}_i \cdot \frac{\partial W}{\partial p_i} \]
\[ = \sum_i \frac{p_i}{W} \cdot \left( \frac{\partial W}{\partial p_i} \right)^2 - \sum_i p_i \frac{\partial W}{\partial p_i} \]
\[ = \frac{1}{W} \left[ \sum_i p_i \cdot \left( \frac{\partial W}{\partial p_i} \right)^2 \sum_j p_j - \sum_i p_i \frac{\partial W}{\partial p_i} \cdot \sum_j p_j \frac{\partial W}{\partial p_j} \right] \]
\[ = \frac{1}{W} \left[ \sum_{i<j} p_i p_j \left( \frac{\partial W}{\partial p_i} - \frac{\partial W}{\partial p_j} \right)^2 \right] \geq 0 \] (14)

Thus, in this case, we construct the adaptive landscape for the non-gradient model in Eq. 7 as

\[ \phi(q) = W(q) = 1 + 2q_1s_1 + (q_2 + q_1^2)(s_2 - 2s_1). \] (15)

The other two dynamical factors are:

\[ D = \begin{pmatrix} D_{11} & 0 \\ 0 & D_{11} \end{pmatrix}, \quad Q = \begin{pmatrix} 0 & -Q_{21} \\ Q_{21} & 0 \end{pmatrix} \] (16)

according to Eq. 5 and Eq. 6. We list the analytical expressions for $D_{11}$ and $Q_{21}$ in Appendix C.

The adaptive landscape exists for this non-gradient case. The dynamical factor $Q \neq 0$, and it leads to that the evolution path deviates from the gradient of the adaptive landscape, as we illustrate in Fig. 1. As in this example, the possible existence of the dynamical factor
Figure 2: (Color online) Single peak case. We plot the adaptive landscape $\phi$, the vector field $f$ of the system, its dissipative part $f_d$, and its conservative part $f_c$. The red regions are of high adaptiveness and the blue regions are of low adaptiveness. Parameter settings are: $s_1 = 0.08$, $s_2 = 0.1$, $r = 0$.

$Q$ demonstrates that the gradient criterion is generally irrelevant to to the existence of the adaptive landscape.

After analyzing the structure of the adaptive landscape (we put the analysis in Appendix E), we find that the adaptive landscape has a single peak as the global stable state at $(1,0)$, when $-1 < s_1 < s_2$, $0 < s_2$, and $r = 0$. We illustrate the adaptive landscape $\phi$, the vector field $f$ of the system, its dissipative part $f_d$, and its conservative part $f_c$ in Fig. 2 with $s_1 = 0.08$, and in Fig. 3 with $s_1 = -0.01$.

In this case, it is applicable for the mean fitness to be a candidate for the adaptive landscape, because the Lyapunov property is preserved under the coordinate transformation, or in other words, under different representations, but the gradient criterion simply excludes them all, which shows another aspect of the limitation about the gradient criterion.

4.2. Case 2: Asymmetric selective advantage ($s_2 > s_1 > 0$): single peak case

In the current case, we observe that there is always a tendency to increase ($f_1(q) \geq 0$) for the allele frequency $q_1$ in the phase space in Eq. 8 (we provide the proof in Appendix E). We construct the adaptive landscape as

$$\phi(q) = q_1,$$  (17)
Figure 3: (Color online) Single peak case. We plot the adaptive landscape $\phi$, the vector field $f$ of the system, its dissipative part $f_d$, and its conservative part $f_c$. The red regions are of high adaptiveness and the blue regions are of low adaptiveness. Parameter settings are: $s_1 = -0.01$, $s_2 = 0.1$, $r = 0$.

Figure 4: (Color online) Single peak case. We plot the adaptive landscape $\phi$, the vector field $f$ of the system, its dissipative part $f_d$, and its conservative part $f_c$. The red regions are of high adaptiveness and the blue regions are of low adaptiveness. Parameter settings: $s_1 = 0.08$, $s_2 = 0.1$, $r = 0.2$.

which is increasing with $q_1$, and is independent of the variable $q_2$ and the parameters. The analytical expressions of $D$ and $Q$ are:

$$D = \begin{pmatrix} f_1 & 0 \\ 0 & f_1 \end{pmatrix}, \quad Q = \begin{pmatrix} 0 & -f_2 \\ f_2 & 0 \end{pmatrix} \tag{18}$$

according to Eq. 5 and Eq. 6, where $f_1$ and $f_2$ are given in Eq. 7. We illustrate the adaptive landscape $\phi(q)$, the vector field $f$ of the system, its dissipative part $f_d$, and its conservative part $f_c$ in Fig. 4 with recombination $r = 0.2$, and in Fig. 5 with recombination $r = 0$.

Our adaptive landscape construction is consistent with Wright’s proposal: the single peak structure captures the global stability of the population, and it is also consistent with the local stability analysis\cite{29}. The adaptiveness keeps increasing ($\dot{\phi}(q) > 0$), except for three points...
Figure 5: (Color online) Single peak case. We plot the adaptive landscape $\phi$, the vector field $f$ of the system, its dissipative part $f_d$, and its conservative part $f_c$. The red regions are of high adaptiveness and the blue regions are of low adaptiveness. Parameter settings are: $s_1 = 0.08$, $s_2 = 0.1$, $r = 0$.

$A = (0, 0)$, $B = (1, 0)$, and $C = (0.5, -0.25)$ where $\dot{\phi}(q) = 0$. Both $A$ and $B$ are fixed points, while $C$ is a fixed point only if $r = 0$. On the landscape, any positive perturbation ($\Delta q_1 > 0$) will be amplified when the population starts from either $A$ or $C$, which indicates that the points are unstable. The peak $B$ is a global stable point, which is unique in current case.

4.3. Case 3: A typical double peak case when $-1 < s_1 < 0 < s_2$

We do not find analytical expressions for the adaptive landscape in this parameter region. We use the geometry distance of the orbits, defined in Eq. 19, to construct the landscape for the system. We calculate the landscape and other dynamical components numerically.

In the case $(s_1 = -0.01, s_2 = 0.1, r = 0.125)$, the points $A = (0, 0)$, $B = (1, 0)$ are stable fixed points; the point $C$ between $A$ and $B$ is a saddle point. The stable manifold of $C$ separates the space into the left part and the right part. In each part, the geometry length of the orbit from the point $q$ to corresponding stable fixed point is

$$L(q) = \int_0^{+\infty} \|f(s(t, q))\| dt$$

(19)

where $s(0, q) = q$, and $\frac{\partial s}{\partial t}(t, q) = f(s(t, q))$.

The geometry length of the orbit in the left part and in the right has a constant gap on the boundary, which consists of the stable manifold of the saddle $C$. The gap results from the difference between the length from the saddle $C$ to the stable fixed points $A$ and $B$, denoting the geometry lengths as $L_A$ and $L_B$. After subtracting the gap, we construct the adaptive landscape.
landscape as
\[
\phi(q) := \begin{cases} 
-(L(q) - L_A) & \text{if } \lim_{t \to +\infty} q(t) = A; \\
-(L(q) - L_B) & \text{otherwise}.
\end{cases}
\]  
(20)

We prove the continuity of the landscape in Appendix G. The matrices \(D(q)\) and \(Q(q)\) is formally constructed according to Eq. 5 and Eq. 6.

We illustrate the adaptive landscape \(\phi\), the vector field \(f\) of the system, its dissipative part \(f_d\), and its conservative part \(f_c\) in Fig. 6 (global view), and amplify them in Fig. 7 (local view). The boundary of the attractive basins is automatically located by the numerical construction, which is approximately linear\(^{[29]}\).

Figure 6: (Color online) Double peak case. We plot the adaptive landscape \(\phi\) (global view), the vector field \(f\) of the system, its dissipative part \(f_d\), and its conservative part \(f_c\). The red regions are of high adaptiveness and the blue regions are of low adaptiveness. Parameter settings: \(s_1 = -0.01, \ s_2 = 0.1, \ r = 0.125\).

Figure 7: (Color online) Double peak case. We plot the adaptive landscape \(\phi\) (local view), the vector field \(f\) of the system, its dissipative part \(f_d\), and its conservative part \(f_c\). The red regions are of high adaptiveness and the blue regions are of low adaptiveness. Parameter settings: \(s_1 = -0.01, \ s_2 = 0.1, \ r = 0.125\).
5. Discussion

The adaptive landscape is one of the fundamental concepts in the population genetics and other fields, even Wright himself had been discussing this concept for more than half a century\cite{1,4}. Its importance is supported by the abundant works that take use of this notion to characterize diverse phenomena\cite{1−20}. In the recent textbook by Ewens\cite{30}, Wright’s theory is summarized as: “Wright proposed a three-phase process under which evolution could most easily occur. This view assumes that large populations are normally split up into semi-isolated subpopulations, or demes, each of which is comparatively small in size. Within each deme there exists a genotypic fitness surface, depending on the genetic constitution at many loci, and in conformity with the ‘increase in mean fitness’ concept, gene frequencies tend to move so that local peaks in this surface are approached. The surface of mean fitness is assumed to be very complex with multiplicity of local maxima, some higher than others. If a full deterministic behavior obtains the system simply moves to the nearest selective peak and remains there. The importance of the comparatively small deme size is that such strict deterministic behavior does not occur: random drift can move gene frequencies across a saddle and possibly under the control of a higher selective peak. Random changes in selective values can also perform the same function.”

In the quantitative framework\cite{9,16}, the adaptive landscape is incorporated into the decomposition of the dynamics. Consistent with Wright’s theory and the above summary, the non-decrease of the adaptiveness corresponds to the Lyapunov property in mathematics and engineering. The decomposition in Eq. 2 suggests that, for systems beyond the gradient systems, three components jointly determine the motion. We have constructed the adaptive landscapes for the 2-d evolution model where the adaptive landscape was thought not to exist, based on the violation of the gradient criterion \((\nabla \times f(q) = 0)\). With our constructions, we have observed that the anti-symmetric matrix \(Q \neq 0\) in these cases. The conservative part \(f_c\) deflects the population from the gradient direction of the adaptive landscape. Therefore, the gradient criterion generally fails and is irrelevant to the existence of the adaptive landscape. In addition, we have proved that the Lyapunov property can be preserved during the coordinate transformation, such as in the Case 1, which has shown another aspect of the mathematical convenience and soundness.

The framework\cite{9,16} has been systematically investigated in linear dynamics\cite{36}, in typical
types of non-gradient dynamics\textsuperscript{[37–40]}, in a real genetic switch system\textsuperscript{[12]}, and is supported by a physical experiment\textsuperscript{[24]}, with which we may expect the framework to be applicable for more general dynamics. The general mathematical proof of the framework remains an open problem, but we emphasize that our constructions and results for the concrete model do not rely on the general proof of the framework.

The evolution and other nonequilibrium phenomena generally can be modeled by a set of stochastic differential equations\textsuperscript{[14,16,17,25]}, and the selection of the type of the stochastic integration has been a subtle problem\textsuperscript{[14,41,42]}. For example, Jin Wang’s framework\textsuperscript{[17]} and Hong Qian’s work\textsuperscript{[25]} choose the types of stochastic integration different from Ping Ao’s framework\textsuperscript{[16]}, but they come to the same end at the zero noise limit (the noise strength approaches zero), where Ao’s decomposition remains valid. Therefore, Wang’s and Qian’s works support the soundness of Ao’s decomposition. In Qian’s work, the equations of the system and the steady state distribution, which fully characterize the stochastic dynamics, have been stated\textsuperscript{[25]} to be consistent with Ao’s framework. The conservative part $g(q)$ in Qian’s work corresponds to the conservative part $f_c = \pm Q(q) \cdot f(q)$ in Ao’s framework, and is required\textsuperscript{[25]} to be not only vertical to $\nabla \phi(q)$ which is the same in Ao’s decomposition, but also is required to be divergence free $\nabla \cdot g = 0$. Therefore, the systems discussed in Qian’s work is restricted to a special class of dynamics, which cannot imply any limitation about Ao’s framework. We put the mathematical details in Appendix H.

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Appendix

A Verification about dissipation and conservation

In Eq. 2, \( f_\text{d} = D(q)\nabla \phi \) can be called the dissipative part, which contributes to the increase of the adaptiveness and drives a system to more stable states:

\[
(\nabla \phi(q))^\top f_\text{d}(q) = (\nabla \phi(q))^\top D(q)\nabla \phi(q) \geq 0 .
\]  

(A-1)

The other part \( f_\text{c}(q) = Q(q)\nabla \phi(q) \) can be called the conservative part, which does not change the adaptiveness (its direction is always perpendicular to the gradient direction of the adaptive landscape):

\[
(\nabla \phi(q))^\top f_\text{c}(q) = (\nabla \phi(q))^\top Q(q)\nabla \phi(q) = 0 .
\]  

(A-2)
Together we have

\[ \dot{\phi}(q) = (\nabla \phi(q))^\tau \cdot f(q) = (\nabla \phi(q))^\tau [D(q) + Q(q)] \nabla \phi(q) = (\nabla \phi(q))^\tau D(q) \nabla \phi(q) \geq 0 . \quad (A-3) \]

B Original biological model

In the work\cite{24}, the model in Eq. 7 is expressed in notations \( p \) and \( D \) instead of \( q_1 \) and \( q_2 \). Using the original notations, the model is expressed as follows:

\[
\dot{p} = \frac{\{D[s_2 - s_1 - p(s_2 - 2s_1)] + (1 - p)p[p(s_2 - 2s_1) + s_1]\}}{1 + 2ps_1 + (D + p^2)(s_2 - 2s_1)} , \quad (A-4)
\]
\[
\dot{D} = \frac{\{D(1 + s_2) - [2Dp(1 - p) - D^2 - p^2(1 - p)^2](s_2 - 2s_1 - s_1^2)](1 - r) - D}{[1 + 2ps_1 + (D + p^2)(s_2 - 2s_1)]^2} . \quad (A-5)
\]

C Dynamical factors in the case \( r = 0 \)

We list the expressions of \( D_{11} \) and \( Q_{21} \) as follows:

\[
D_{11} = \left[ \frac{2(s_1 - 2q_1s_1 + q_1s_2)[q_2((-1 + 2q_1)s_1 + s_2 - q_1s_2) + (1 - q_1)q_1(s_1 - 2q_1s_1 + q_1s_2)]}{1 + 2q_1s_1 + (q_2 + q_1^2)(-2s_1 + s_2)} + \right. \\
\left. \quad (-2s_1 + s_2)\right] - q_2 + \frac{-[q_2 + (-1 + q_1)q_1]^2(2s_1 + s_1^2 - s_2) + q_2(1 + s_2)}{1 + 2q_1s_1 + (q_2 + q_1^2)(-2s_1 + s_2)^2} - \\
\left. \quad r\left[ -\left( q_2 + (-1 + q_1)q_1 \right)^2(2s_1 + s_1^2 - s_2) + q_2(1 + s_2) \right] \right] \\
\left. \quad (1 + 2q_1s_1 + (q_2 + q_1^2)(-2s_1 + s_2)^2) \right] \\
\left. \quad \left[ (-2s_1 + s_2)^2 + 4(s_1 - 2q_1s_1 + q_1s_2)^2 \right] \right] \quad (A-6)
\]
and
\[
Q_{21} = \left[ -\frac{(-2s_1 + s_2)q_2\left((1 + 2q_1)s_1 + s_2 - q_1 s_2\right) + (1 - q_1)q_1(s_1 - 2q_1 s_1 + q_1 s_2)}{1 + 2q_1 s_1 + (q_2 + q_1^2)(-2s_1 + s_2)} \right] + \\
\frac{2(s_1 - 2q_1 s_1 + q_1 s_2)\left[-q_2 + \frac{-q_2 + (-1 + q_1)q_1^2\left(2s_1 + s_1^2 - s_2\right) + q_2(1 + s_2)}{1 + 2q_1 s_1 + (q_2 + q_1^2)(-2s_1 + s_2)}\right]}{\left((-2s_1 + s_2)^2 + 4(s_1 - 2q_1 s_1 + q_1 s_2)^2\right)}
\]

\[\text{(A-7)}\]

## D Coordinate-invariance of the Lyapunov property

We show that the Lyapunov property is preserved under the coordinate transformation. Suppose that the deterministic system Eq. 1 can be mapped to another dynamical system by a differentiable coordinate transformation
\[
y = h(q) , \quad \text{(A-8)}
\]

Suppose that \(q(t)\) is a trajectory in the original system, \(\phi(q)\) is the Lyapunov function for the original system, and \(y(t) = h(q(t))\) is the corresponding trajectory in the new system. We prove that the function \(\psi(y)\) defined as
\[
\psi(y) := \phi(h^{-1}(y)). \quad \text{(A-9)}
\]
is a Lyapunov function for the new system \(y(t)\). Pick any trajectory \(y(t)\), two positions \(y\) and \(y'\) at two different times \(t > t'\). Denote \(q = h^{-1}(y)\) and \(q' = h^{-1}(y')\). The Lyapunov property of \(\phi\) for the original system implies that:
\[
\phi(q) \geq \phi(q') \Rightarrow \phi(h^{-1}(y)) \geq \phi(h^{-1}(y')) \Rightarrow \psi(y) \geq \psi(y') \quad \text{(A-10)}
\]
which shows that \(\psi(y)\) is a Lyapunov function for the new system \(y(t)\).
E Analysis structure of landscape \((r = 0)\)

The landscape in Eq. 15 is expressed as \(\phi(q) = W(q) = 1 + 2q_1s_1 + (q_2 + q_1^2)(s_2 - 2s_1)\). The parameter region for \(s_1\) and \(s_2\) is in Eq. 9; the variable region for \(q\) is in Eq. 8. The gradient is

\[
\frac{\partial \phi(q)}{\partial q_1} = 2s_1 + 2q_1 \cdot (s_2 - 2s_1), \\
\frac{\partial \phi(q)}{\partial q_2} = s_2 - 2s_1 .
\] (A-11)

\(s_1 \geq 0\)

1) \(s_2 > 2s_1 \geq 0, s_2 > 0\): the landscape takes its maximal value on the upper boundary \(\{q \mid q_2 = q_1(1 - q_1)\}\). And the landscape \(\phi(q) = 1 + 2q_1s_1 + [q_1(1 - q_1) + q_1^2] \cdot (s_2 - 2s_1) = 1 + q_1s_2\) takes its maximal at \((1, 0)\).

2) \(s_2 = 2s_1\): the landscape \(\phi(q) = 1 + q_1s_2\) takes its maximal at \((1, 0)\).

3) \(0 < s_1 < s_2 < 2s_1\): the landscape takes its maximal value on the lower boundary \(q_2 = \text{Max}[-q_1^2, -(1 - q_1)^2]\). Piecewise analysis leads to that the landscape takes its global maximal at \((1, 0)\).

4) \(-1 < s_1 < 0\)

The landscape \(\phi(q)\) takes its maximal on the upper boundary \(q_2 = q_1(1 - q_1)\), because \(s_2 > 0 > s_1\). On the upper boundary, \(\phi(q) = 1 + q_1s_2\) has only one peak at \((1, 0)\).

In conclusion, the landscape \(\phi(q)\) has a single peak in Case 1.

F Analytical construction \((s_2 > s_1 > 0)\)

We prove that \(\phi(q) = q_1\) is always non-decreasing inside the region in Eq. 8

\[
\dot{\phi} = \nabla \phi \cdot f = \frac{\partial \phi}{\partial q_1} f_1 + \frac{\partial \phi}{\partial q_2} f_2 \\
= f_1 = \frac{q_2[s_2 - s_1 - q_1(s_2 - 2s_1)] + (1 - q_1)q_1[q_1(s_2 - 2s_1) + s_1]}{1 + 2q_1s_1 + (q_2 + q_1^2)(s_2 - 2s_1)}
\] (A-12)

For the numerator of Eq. (A-12)

When \(0 \leq q_1 \leq 0.5\), take use of \(q_2 \geq -q_1^2\):

Numerator \(\geq -q_1^2[s_2 - s_1 - q_1(s_2 - 2s_1)] + (1 - q_1)q_1[q_1(s_2 - 2s_1) + s_1] = (1 - 2q_1)q_1s_1 \geq 0\)
When $0.5 \leq q_1 \leq 1$, take use of $q_2 \geq -(1 - q_1)^2$:

\[
\text{Numerator} \geq -(1 - q_1)^2[s_2 - s_1 - q_1(s_2 - 2s_1)] + (1 - q_1)q_1[s_2 - 2s_1 + s_1] = (1 - q_1)(2q_1 - 1)(s_2 - s_1) \geq 0
\]

For the denominator of Eq. A-12

When $0 \leq q_1 \leq 0.5$,

\[
\text{Denominator} \geq 1 + 2q_1s_1 - (q_2 + q_1^2) \cdot s_1 \\
\geq 1 + 2q_1s_1 - q_1^2s_1 - q_2s_1 \\
\geq 1 + 2q_1s_1 - q_1^2s_1 - q_1(1 - q_1)s_1 = 1 + q_1s_1 > 0
\]

When $0.5 \leq q_1 \leq 1$ and $s_2 \geq 2s_1$,

\[
\text{Denominator} \geq 1 + 2q_1s_1 + (-1 - q_1^2 + q_1^2) \cdot (s_2 - 2s_1) = 1 + 2q_1s_1 + (2q_1 - 1) \cdot (s_2 - 2s_1) > 0
\]

When $0.5 \leq q_1 \leq 1$ and $s_1 < s_2 < 2s_1$,

\[
\text{Denominator} \geq 1 + 2q_1s_1 + (q_1(1 - q_1) + q_1^2) \cdot (s_2 - 2s_1) = 1 + 2q_1s_1 + q_1(s_2 - 2s_1) = 1 + q_1s_2 > 0
\]

In all, the Eq. A-12 is non-negative in Case 2. So $\phi = q_1$ is a adaptive landscape.

**G  Numerical construction in the case $-1 \leq s_1 < 0 < s_2$ and $r \neq 0$**

Consider a point $q_0$ on the left part. The orbits $s(t, q)$ starting at $q$ in the neighborhood $\mathcal{O}_0$ of $q_0$ will all converge to the stable fixed point $A$ according to the Poincaré–Bendixson theorem\(^{[43]}\).

For any given $\epsilon > 0$, select a neighborhood $\mathcal{O}_A$ of $A$ such that $s(t + T, q)$ will be in $\mathcal{O}_A$ for all $q \in \mathcal{O}_0$, $t > 0$, and a fixed $T > 0$. Inside the neighborhood $\mathcal{O}_A$, there are constants $c, K > 0$ satisfying\(^{[44]}\)

\[
\|s(t + T, q)\| \leq K\|s(T, q)\|e^{-ct}.
\]
Inside $\mathcal{O}_A$, the integration is dominated by the linearized part $Df_A$ at $(0,0)$ which is assumed to be non-degenerated, and there is a constant $c' > 0$ that

$$
\int_T^{+\infty} \|f(s(t,q))\| dt \\
\leq \int_T^{+\infty} c' \|Df_A \cdot s(t,q)\| dt \\
\leq \int_T^{+\infty} c' \|Df_A\| \cdot \|s(t,q)\| dt \\
\leq \int_0^{+\infty} c' \|Df_A\| \cdot K \|s(T,q)\| e^{-ct} dt \\
= c' K \cdot \|Df_A\| \cdot \|s(T,q)\| \int_0^{+\infty} e^{-ct} dt \\
= c' K \cdot \|Df_A\| \cdot \|s(T,q)\|.
$$

Choose the neighborhood $\mathcal{O}_A$ with radius smaller than $\frac{c}{4c'K \cdot \|Df_A\|} \epsilon > 0$. Because the flow is continuous with respect to $t \times q$, the neighborhood $\mathcal{O}_0$ can be also selected small enough such that

$$
\left| \int_0^T \|f(s(t,q_1))\| dt - \int_0^T \|f(s(t,q_2))\| dt \right| \leq \frac{\epsilon}{2}
$$

where $q_1, q_2 \in \mathcal{O}_0$. In all, $|L(q_0) - L(q)| < \epsilon$ for all $q \in \mathcal{O}_0$, therefore $L(q)$ is continuous at $q_0$.

Near the boundary between the left part and the right part, which is the stable manifold of the saddle $C$, the orbit will first follow the stable manifold to the neighborhood of the saddle, then to either $A$ or $B$ following the unstable manifold of the saddle. Thus, there is a constant gap of the geometry length from the left side and the right sides. The constant gap has been revised in Eq. 20 by subtracting the saddle-to-stable length: either $L_A$ or $L_B$, depending on whether it is on the left side or on the right side.

## H Mathematical Details of the Discussion Section

A nonequilibrium system is described by a set of stochastic differential equations \textsuperscript{[14,16,17,25]}:

$$
\dot{q} = f(q) + \xi(q,t)
$$

(A-13)
where $q, f(q), \xi(q,t)$ are n-dimension vectors, and the noise part $\xi(q,t)$ is the Gaussian white noise here, characterized by the zero mean $\langle \xi_i(q,t) \rangle = 0$ and its covariance

$$\langle \xi(q,t)\xi^T(q,t') \rangle = 2\theta D(q)\delta(t-t')$$

(A-14)

where $\theta > 0$ is the strength of noise, $\delta(\cdot)$ is the Dirac delta function, $D(q) \in \mathbb{R}^{n \times n}$ is the (semi-positive definite) diffusion matrix which can be regarded as the structure of the noise in the phase space.

The steady state distribution is generally assumed as

$$\rho_\infty(q,\theta) = N(q)Z(\theta) \cdot \exp \left[ -\frac{\phi(q)}{\theta} + O(\theta) \right]$$

(A-15)

which works well in practice when $\theta$ is small, where $N(q)Z(\theta)$ is the normalizer, $\phi(q)$ is the potential function.

Substrate the steady state distribution into the (Ito’s, $\alpha = 1$ type, Stratonovich’s, A-type) Fokker-Planck equation (FPE). The terms equal zero according to orders of $\theta$, and the first term leads to the general equation

$$(\nabla \phi(q))^T \cdot [f(q) + D(q) \cdot \nabla \phi(q)] = 0,$$

(A-16)

which is independent of the integration types, and is a generally valid equation. The above equation is essentially the same with Eq. [4], because the adaptive landscape in biology takes an opposite sign with the potential function in physics.

In Qian’s work[25], Qian defines a stationary current in his Eq. 19:

$$J(q)e^{\phi(q)} = G(q)S(q)G^T(q)\nabla \phi(q) - G(q)\nabla \phi(q)$$

where $\phi$ is the potential function, $D(q) = G(q)S(q)G^T(q)$ is the diffusion matrix, and $f(q) = -G(q)\nabla \phi(q)$ is the deterministic part. And Qian derives a current relation in his Eq. 20:

$$(\nabla \phi(q))^T \cdot J(q)e^{\phi(q)} = 0$$

$$= (\nabla \phi(q))^T \cdot [G(q)S(q)G^T(q)\nabla \phi(q) - G(q)\nabla \phi(q)]$$

$$= (\nabla \phi(q))^T \cdot [D(q)\nabla \phi(q) + f(q)]$$

which is equivalent to the Eq. [A-16]. Thus, no restriction can be found from the generally valid relation.
In the rest of this section, we derive Eq. [A-16] for typical types of stochastic integration.

Ito’s FPE is

\[
\frac{\partial}{\partial t} \rho(q,t) = -\sum_i \partial_i [f_i(q) \rho(q)] + \theta \sum_{i,j} \partial_i \partial_j [D_{ij}(q) \rho(q)].
\] (A-17)

Substitute the steady state distribution in Eq. [A-15] into Eq. [A-17], we get

\[
\frac{\partial}{\partial t} \rho(q,\infty) = 0
\]

\[
= -\sum_i \partial_i [f_i(q) \rho_\infty(q)] + \theta \sum_{i,j} \partial_i \partial_j [D_{ij}(q) \rho_\infty(q)] + \theta \sum_{i,j} \left[ \rho_\infty(q) \partial_i \partial_j D_{ij}(q) + \partial_i D_{ij}(q) \partial_j \rho_\infty(q) + \partial_j D_{ij}(q) \partial_i \rho_\infty(q) + D_{ij}(q) \partial_i \partial_j \rho_\infty(q) \right]
\]

\[
= \rho_\infty(q) \left\{ -\sum_i \left\{ \partial_i f_i(q) + f_i(q) \left[ \partial_i N(q) + \frac{-\partial_i \phi(q)}{\theta} \right] \right\} \right\}
\]

\[
+ \theta \sum_{i,j} \left\{ \partial_i \partial_j D_{ij}(q) + \partial_i D_{ij}(q) \left[ \partial_j N(q) + \frac{-\partial_j \phi(q)}{\theta} \right] \right\}
\]

\[
+ \partial_j D_{ij}(q) \left[ \partial_i N(q) + \frac{-\partial_i \phi(q)}{\theta} \right] + D_{ij}(q) \left[ \partial_i N(q) \partial_j N(q) + \frac{-\partial_i \phi(q)}{\theta} \partial_j N(q) + \partial_i \partial_j N(q) + \partial_i N(q) \partial_j \frac{-\partial_j \phi(q)}{\theta} + \partial_j \frac{-\partial_i \phi(q)}{\theta} + \frac{-\partial_i \partial_j \phi(q)}{\theta} \right] \right\}
\]

The first term of the order \(\frac{\rho_\infty}{\theta}\) should be zero:

\[
\frac{\rho_\infty}{\theta} \left[ \sum_i f_i(q) \partial_i \phi(q) + \sum_{i,j} D_{ij}(q) \partial_i \phi(q) \partial_j \phi(q) \right] = 0
\] (A-18)

which leads to the Eq. [A-16].

The \(\alpha = 1\) type FPE is

\[
\partial_t \rho(q,t) = -\sum_i \partial_i [f_i(q) \rho(q)] + \theta \sum_{i,j} \partial_i [D_{ij}(q) \partial_j \rho(q)].
\] (A-19)
Substitute the steady state distribution in Eq. A-15 into Eq. A-19, we get

\[ \partial_t \rho(q, \infty) = 0 \]

\[ = - \sum_i \partial_i [f_i(q) \rho_\infty(q)] + \theta \sum_{i,j} \partial_i [D_{ij}(q) \partial_j \rho_\infty(q)] \]

\[ = - \sum_i [\rho_\infty(q) \partial_i f_i(q) + f_i(q) \partial_i \rho_\infty(q)] + \theta \sum_{i,j} \left[ \partial_i D_{ij}(q) \partial_j \rho_\infty(q) + D_{ij}(q) \partial_i \partial_j \rho_\infty(q) \right] \]

\[ = \rho_\infty(q) \left\{ - \sum_i \left\{ \partial_i f_i(q) + f_i(q) \left[ \partial_i N(q) + \frac{-\partial_i \phi(q)}{\theta} \right] \right\} \right. \]

\[ + \left. \theta \sum_{i,j} \left\{ \partial_i D_{ij}(q) \left[ \partial_j N(q) + \frac{-\partial_j \phi(q)}{\theta} \right] \right. \right. \]

\[ + \left. D_{ij}(q) \left[ \partial_i N(q) \partial_j N(q) + \frac{-\partial_i \phi(q)}{\theta} \partial_j N(q) + \partial_i \partial_j N(q) + \partial_i N(q) \frac{-\partial_j \phi(q)}{\theta} + \frac{-\partial_i \phi(q)}{\theta} - \frac{-\partial_j \phi(q)}{\theta} + \frac{-\partial_i \partial_j \phi(q)}{\theta} \right] \right\} \]

The first term of the order \( \frac{\rho_\infty}{\theta} \) should be zero, which also leads to the Eq. A-16.

The proof for Stratonovich’s integration is similar to above derivations.

For A-type integration, the Boltzmann-Gibbs distributions exactly stands. The dynamics is decomposed as\(^{[10]}\):

\[ f(q) = -[D(q) + Q(q)] \nabla \phi(q) \quad \text{(A-20)} \]

where \( Q \) is an anti-symmetric matrix. Multiply both sides with \( \nabla^r \phi(q) \), resulting in the Eq. A-16.