

Geometric phase in the Crow-Kimura model of molecular evolution on dynamic environments

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When taking place under fluctuating environments, some classical results of evolutionary dynamics in fitness landscapes need to be reconsidered. Under such nonequilibrium conditions, the properties of adaptive evolution might escape from the expectations grounded in equilibrium systems. Here, an important contribution to this nonequilibrium dynamics results from the presence of a geometry (Berry) phase in the Crow-Kimura model of molecular evolution with asymmetric mutations. By considering changes in fitness alone as well as changes in both fitness and mutation, analytical expressions for the Berry phase are derived, showing strong singularities at bulk transition points. Periodically varying parameters are also analyzed for the two-dimensional case. The potential implications for evolutionary and prebiotic scenarios are discussed.

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I. INTRODUCTION

In the standard picture of mutation-selection models of evolution, from Wright-Fisher's early work to the Crow-Kimura and Eigen models of quasispecies [1–9], the population dynamics is described in terms of changes of gene frequency distributions. Such models have been very effective to describe a broad range of scenarios, from virus transfer experiments to genomic changes. Typically, most relevant results involve the mean fitness and the second moments of the equilibrium genotype distributions. However, the constancy of mutation and selection parameters during the evolutionary process is a rather special limiting case. In this context, under nonequilibrium scenarios, such as environmental changes with a timescale faster than the mutation-selection one, new types of phase transitions can emerge [10], including changes in the error thresholds in quasispecies. In this case, we have to look for the fitness flows taking place in dynamic fitness seascapes [11].

The theoretical exploration of fluctuating fitness landscapes has revealed a very rich phenomenology [12–21]. In the current article, we focus on the presence of a *geometric* contribution to the selection rate, as described in terms of a Berry phase, in the Crow-Kimura (CK) model. The Berry phase has been recently explored within the context of simple,

stochastic evolutionary ecology models [22–27]. One crucial result from these works is that, in dynamical environments, the relative fitness is not equal to the geometric average of the fitness over each environment but depends on the *sequence* of environments. Specifically, in a cyclic, slowly varying environment, an extra contribution to fitness is obtained from the oriented area enclosed by the system's trajectory in the environment state space. Here, we derive an analytical expression for the geometric phases in the CK model and investigate the case of asymmetric mutations when a nonzero phase arises.

In order to introduce the Berry phase, we will first define the evolution model using some parameters $\mathbf{k}$. These parameters can include a whole range of key features, including growth rates (for a given fitness function) and mutations. The evolving population has a current fitness $R(\mathbf{k}, t)$, and the steady state fitness will be indicated as $R_0(\mathbf{k})$ (which would correspond to a state satisfying the condition of detailed balance). The evolutionary equivalent to the Berry phase equivalent is defined as the circuit integral,

$$\Delta = \oint_{\gamma} [R(\mathbf{k}, t) - R_0(\mathbf{k})] d\mathbf{k} \equiv \oint_{\gamma} \delta \Delta, \quad (1)$$

where the integration is performed along some loop γ . Here, Δ along the closed trajectory is nonzero in quantum mechanics (QM) when there are monopolelike terms in the effective Hamiltonian, and R in (1) is replaced by the energy of the system. In QM, the noncommutative nature of linear operators is essential for bringing nonzero Δ values.

Within the evolutionary context, we have some analogous features that provide the equivalent of the noncommutative behavior, due to the nature of selection, mutation, recombination, as well as competition (that constrains population size). The key point is that in a time-dependent fitness

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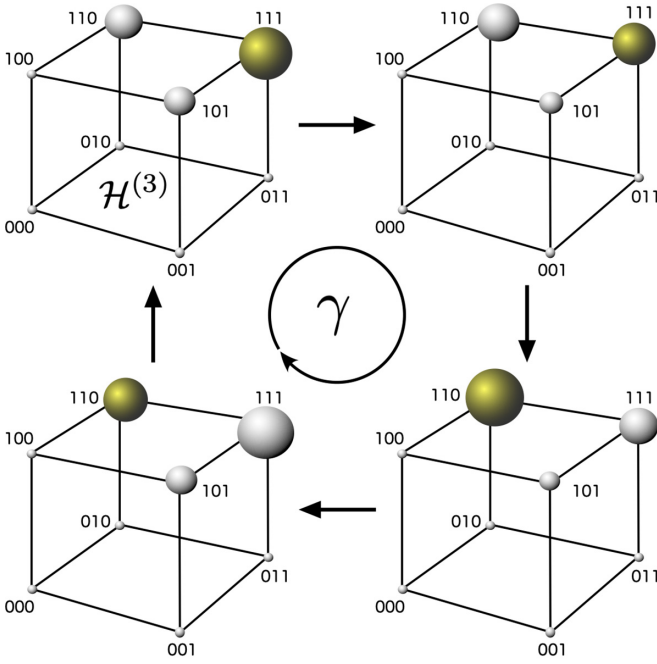


FIG. 1. A low-dimensional view of the dynamics for an $L = 3$ genome in the CK model with a changing fitness landscape. Here, the location of the local fitness maximum is indicated in color, while the diameter of the spheres scales with fitness. A cyclic change is shown, where two strings (110 and 111) can be associated to the optimum in different times.

landscape, time-dependent selection coefficients are expected to occur, see Fig. 1, to occur, leading to path-dependent effects and a fitness flux. Such a changing landscape would be expected for fluctuating environments (including periodic ones) as well as cycles of selection where mutation rates change, as it occurs in mutator genes within microbial populations [25–27]. Specifically, the value and sign for the previous expression will provide a measure of the evolutionary responses to the environmental changes.

The paper is organized as follows. In Sec. II we define the CK model. In Sec. III we solve the dynamics for the static landscape with asymmetric mutations, as well as the dynamics on a dynamical landscape. In Sec. IV we calculate the Berry phase for different sets of parameters (both demographic and involving mutations) of the model.

II. THE CROW-KIMURA MODEL

The CK model is the simplest version of a many-gene molecular evolution model with nonzero epistasis (i.e., the fitness is a nonlinear function of the fraction of different genotypes). For simplicity, we consider a biallelic model with L loci. In other words, we consider genomes as L -dimensional strings where the i th genome S_i is given by $S_i = (s_i^1, \dots, s_i^L) \in \mathcal{H}^{(L)}$. Here, $\mathcal{H}^{(L)}$ is the sequence space. Hereafter, we denote the allele type as spin variables, namely $s_i^k = \pm 1$ and the space of possible genomes includes 2^L different sequences. We denote different sequences via an index $0 \leq i \leq 2^L - 1$. We choose the (master) sequence S_m with $s_i^m = +1$ for all the alleles as a reference sequence.

The mutation rate from the $+1$ allele to the -1 allele equals μ_1/L while the inverse mutation rate is μ_2/L . In other words, we have $\mu_1 = LP(s_i^j = +1 \rightarrow s_i^j = -1)$ and $\mu_2 = LP(s_i^j = -1 \rightarrow s_i^j = +1)$. Moreover, the fitness r_l of the sequence with a total number of $l-1$ alleles equals $r_l \equiv f(x)$, $x = 1 - 2l/L$, where $f(x)$ is the fitness function. For such a symmetric case we get the following equation for the probability $\hat{p}_l$:

$$\frac{d\hat{p}_l(t)}{dt} = \left(f(x_l, t) - \frac{\mu_1(L-l) + l\mu_2}{L} - R(t) \right) \hat{p}_l(t) + \hat{p}_{l-1} \frac{L-l+1}{L} \mu_1 + \hat{p}_{l+1} \frac{l+1}{L} \mu_2, \quad (2)$$

where the mean fitness is $R = \sum_l \hat{p}_l r_l$. For the $l = 0$ in Eq. (2) we drop the $\hat{p}_{l-1}$ term and for $\hat{p}_{l+1}$ we drop the $\hat{p}_{l+1}$ term. The coefficients $\frac{L-l+1}{L}$, $\frac{l+1}{L}$ arise due to combinatorics [2].

Equation (2) is a nonlinear equation. Using a nonlinear mapping

$$\hat{p}_l = \frac{p_l}{\sum_l p_l}, \quad (3)$$

we get

$$\frac{dp_l(t)}{dt} = \left(f(x_l, t) - \frac{\mu_1(L-l) + l\mu_2}{L} - R(t) \right) p_l(t) + p_{l-1} \frac{L-l+1}{L} \mu_1 + p_{l+1} \frac{l+1}{L} \mu_2. \quad (4)$$

III. THE SOLUTION OF THE DYNAMICS FOR ASYMMETRIC MUTATIONS

A. The Hamilton-Jacobi equation and the static solution

In order to find the dynamical equations for the dynamics of the probability distribution, a Hamilton-Jacobi approach is taken. Following previous work, we make an ansatz $p_l = \exp[Lu(x)]$ where $x = 1 - 2l/L$ and get from Eq. (4),

$$\frac{\partial u}{\partial t} = f(x) + \frac{1+x}{2} \mu_1 e^{2p} + \frac{1-x}{2} e^{-2p} \mu_2 - \frac{1+x}{2} \mu_1 - \frac{1-x}{2} \mu_2, \quad (5)$$

where $p = u'_x$. In the steady state, we consider an ansatz

$$u = Rt + u_0(x),$$

and denoting $p = u'_0$, we obtain

$$\begin{aligned} R_1 &= \max \left(f_1(x) + \sqrt{1-x^2} \sqrt{\mu_1 \mu_2} - \frac{1+x}{2} \mu_1 - \frac{1-x}{2} \mu_2 \right)_x \\ &= f(m) + 4\sqrt{1-m^2} \sqrt{\mu_1 \mu_2} - \frac{1+m}{2} \mu_1 - \frac{1-m}{2} \mu_2, \\ f'_1(m) - \frac{m}{\sqrt{1-m^2}} \sqrt{\mu_1 \mu_2} - \frac{\mu_1 - \mu_2}{2} &= 0, \\ R_1 &= f_1(x) + \frac{1+x}{2} \mu_1 e^{2p} + \frac{1-x}{2} e^{-2p} \mu_2 - \frac{1+x}{2} \mu_1 - \frac{1-x}{2} \mu_2, \end{aligned} \quad (6)$$

where m is just the maximum point and we can look at different solutions and choose the solution with maximal R .

Having an expression for R , we calculate the surplus $s = \sum_i x_i p_i$ from $f(s) = R$. While deriving the last equation, we used the property that the distribution is narrow at the limit of large l , so $\langle r_l \rangle = f(s) + O(1/\sqrt{L})$.

B. The dynamics

The dynamics of the distribution can be calculated using the Hamiltonian equation for the characteristics [28,29]. For our system, we obtain

$$\frac{dx}{dt} = 2 \left(\frac{1+x}{2} \mu_1 e^{2p} - \frac{1-x}{2} \mu_2 e^{-2p} \right), \quad (7)$$

with a constant along the trajectory of characteristics

$$q = f(x) + \frac{1+x}{2} \mu_1 e^{2p} + \frac{1-x}{2} e^{-2p} \mu_2 - \frac{1+x}{2} \mu_1 - \frac{1-x}{2} \mu_2.$$

One can now calculate the distribution at any given point x using the characteristics [6], arriving at the given point x at time t from the initial distribution [6], leading to

$$u(x, t) = u(x_0, 0) + \int_{x_0}^x p dx + qt,$$

and our goal is to simply calculate the dynamics of the maximum of the distribution.

Consider the case when initially the population is focused at some point x_0 . We obtain either one characteristic, i.e.,

$$t = \int_{x_0}^x \frac{1}{2\sqrt{F(x, y)}}, \quad (8)$$

Where we define

$$F(x, y) = \left(f(x) - f(y) + \frac{1+y}{2} \mu_1 + \frac{1-y}{2} \mu_2 \right)^2 - (1-y^2) \mu_1 \mu_2, \quad (9)$$

and the population initially is focused at the point x_0 . For a two-characteristics solution,

$$t = \int_{x_0}^{x_1} \frac{1}{2\sqrt{F(x, y)}} + \int_x^{x_1} \frac{1}{2\sqrt{F(x, y)}}, \quad F(x, x_1) = 0. \quad (10)$$

Let us assume that initially there was a steady state distribution with a fitness function $f_1(x)$ and mean fitness R_1 , and later the new fitness $f_2(x)$ was switched on. At the maximum point x of the distribution, the condition $p = 0$ gives from (8) $q = f(x)$. Thus we should look at the characteristics with $q = f_2(x)$ reaching x at time t from some initial point $X_0(x)$. We are considering a smooth distribution, and thus a smooth change of p . So at $t = 0$ we should take the same $X_0(x)$, p using Eqs. (6) and (8). We are calculating $X_0(x)$ removing p from the system of two

equations,

$$\begin{aligned} f_2(x) &= f_2(x_0) + \frac{1+x_0}{2} \mu_3 e^{2p} + \frac{1-x_0}{2} e^{-2p} \mu_4 \\ &\quad - \frac{1+x_0}{2} \mu_3 - \frac{1-x_0}{2} \mu_4, \\ R_1 &= f_1(x_0) + \frac{1+x_0}{2} \mu_1 e^{2p} + \frac{1-x_0}{2} e^{-2p} \mu_2 \\ &\quad - \frac{1+x_0}{2} \mu_1 - \frac{1-x_0}{2} \mu_2. \end{aligned} \quad (11)$$

In this way we obtain either one characteristic, i.e.,

$$t = \int_{X_0(x)}^x \frac{1}{2\sqrt{F(x, y)}}, \quad (12)$$

or a two-characteristics solution, namely

$$t = \int_{X_0(x)}^{x_1} \frac{1}{2\sqrt{F(x, y)}} + \int_x^{x_1} \frac{1}{2\sqrt{F(x, y)}}, \quad F(x, x_1) = 0. \quad (13)$$

The previous derivations will allow us to analytically calculate the Berry phase, as defined in (1) for the CK model under different scenarios, particularly those involving periodic parameter changes.

IV. THE BERRY PHASE

The circuit integral for the Berry phase will capture, for our evolutionary context, how the fitness deviates from its steady state (i.e., the net deviation from the detailed balance condition). In this context, the sign of Δ will provide a direct indication of fitness changes, namely, (i) when $\Delta > 0$, the population experiences a net increase in fitness over the cycle, indicating that evolution is being driven by a persistent nonequilibrium force in a way that drives adaptation in a preferred direction, and (ii) if $\Delta < 0$, a net decrease in fitness over the cycle will take place, moving the system away from an optimal configuration.

A. The Berry phase for changes in fitness

Now we can go for the problem of defining the geometric phase of the CK model. Consider the slight change in the fitness function, by keeping unchanged μ_1, μ_2 . Equation (11) gives

$$\begin{aligned} f_2(x) - R_2 &= f_2(x_0) - f_1(x_0) - (R_2 - R_1) \\ &\equiv \delta f(x_0) - \delta f(m), \end{aligned} \quad (14)$$

and we used the relations $R_1 = f_1(m)$, $R_2 \approx f_2(m)$.

While differentiating Eq. (9) we get as a dominant term

$$dt/dx = -dX_0/dx \frac{1}{2\sqrt{F(x, X_0)}}.$$

In Eq. (1) for the derivation of Δ there is an integration via dt . Let us change the integration from dt to dx , then from dx to dX_0 . Eventually we get the expression for the geometric phase as

$$\delta \Delta = \int dx (f_2(x) - R_2) = \int_s^m dz \frac{\delta f(z) - \delta f(m)}{2\sqrt{F(s, z)}}, \quad (15)$$

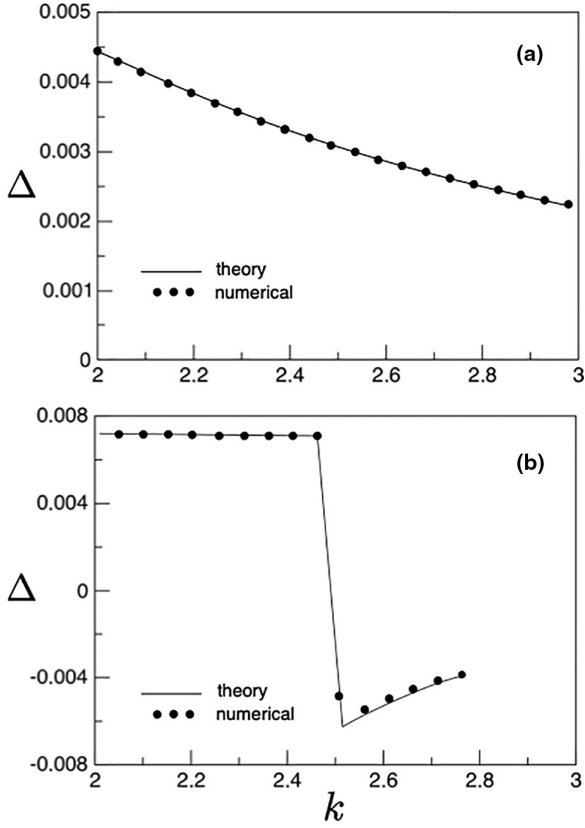


FIG. 2. (a) The geometric phase Δ , numerical vs analytic results, using $f_1(x) = kx^2/2$, $2 \leq k \leq 3$, $f_2(x) = (k + \theta)x^2/2$, $\mu = 1$, where $\theta = 0.05$. In (b) the same plot is displayed, now using $f_1(x) = kx^2$, $f_2(x) = (k + \theta)x^2$. Here, $N = 2 \times 10^3$. The analytic prediction is obtained from Eq. (13), $\mu_2 = 1.5$, $\mu_4 = 1.5$, $\mu_1 = 1$, $\mu_3 = \mu_1 + 0.05(k - 2)$. There is a phase transition at the point $k = 2.55$, with the change of the solution from Eq. (15) to Eq. (16).

where we denote $\delta f(x) = f_2(x) - f_1(x)$. In Fig. 2(a) we display the predicted geometric phase, calculated for some specific choices of the fitness functions for specific μ_i values. Specifically, we consider quadratic and linear growth functions (see Fig. 3). Equation (15) calculates the Berry phase for the simple change from $f_1(x)$ to $f_2(x)$, via a change of the fitness parameter. To derive Eq. (1) we should integrate the expression by Eq. (15) via a loop.

B. The Berry phase for changes in fitness landscape and mutation rates

Although previous studies have also considered periodic fitness changes (where replication rates oscillate over a given timescale) we should also consider the presence of additional regular cycles for mutation rates.

Consider now small changes in the parameter of the fitness function $k \rightarrow k + \delta k$ as well as in the mutation rate, namely $\mu_1 \rightarrow \mu_3 \equiv \mu_1 + \delta\mu_1$, $\mu_2 \rightarrow \mu_4 \equiv \mu_2 + \delta\mu_2$. Let us solve both equations in Eq. (11) for e^{2p} , where the two expressions are equal. In this way we derive the function $X_0(x)$. In this way we derive two branches of

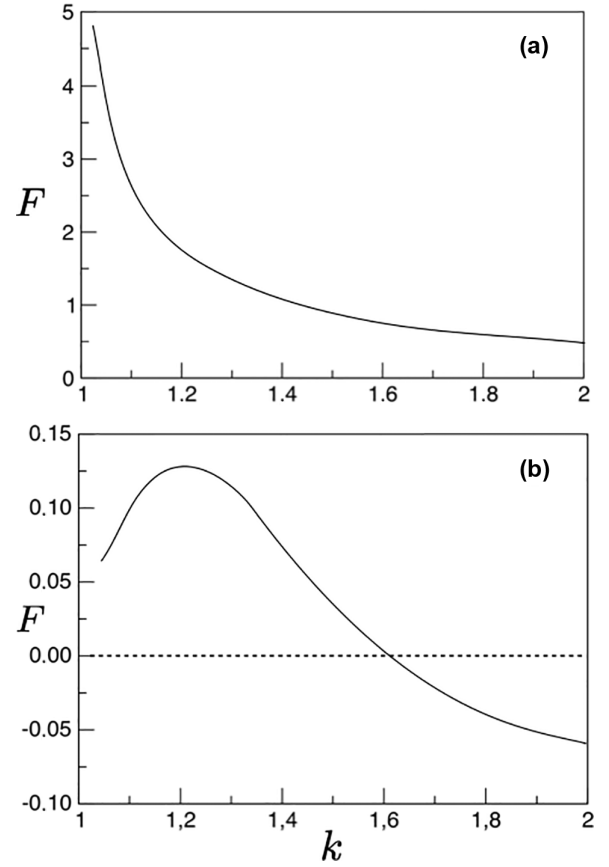


FIG. 3. (a) The Berry phase near the critical point in the CK model with quadratic fitness. The divergence $F \equiv F_{12}$ of the Berry phase is plotted against k , using $f(x) = kx^2/2$, $\mu_1 = \mu_2$. Near the critical point $k = 1$ the Berry phase diverges. (b) F vs the parameter k , with $f(x) = kx$, near the point $\mu_1 = 1$, $\mu_2 = 1$ (no criticality is present here).

solutions:

$$g(x) = \frac{(1-x^2)\left(\frac{d\mu_1}{\mu_2} + \frac{d\mu_2}{\mu_1}\right)}{2[w(x) + W(x)]} + \frac{d\mu_1 W(x)}{\mu_1} + \frac{\delta k x^2}{2} - \frac{1}{2}d\mu_1(x+1) - \frac{1}{2}d\mu_2(1-x). \quad (16)$$

Then for another branch we get

$$g(x) = -\frac{(1-x^2)\left(\frac{d\mu_1}{\mu_2} + \frac{d\mu_2}{\mu_1}\right)}{2[w(x) - W(x)]} + \frac{d\mu_1 d d(x)}{\mu_1} + \frac{\delta k x^2}{2} - \frac{1}{2}d\mu_1(x+1) - \frac{1}{2}d\mu_2(1-x), \quad (17)$$

where

$$\delta\Delta = \int_s^m dy \frac{g(y) - g(m)}{2\sqrt{F(s, y)}},$$

$$w(x) = f(s) - f(x) + (1+x)\frac{\mu_1}{2} + (1-x)\frac{\mu_2}{2},$$

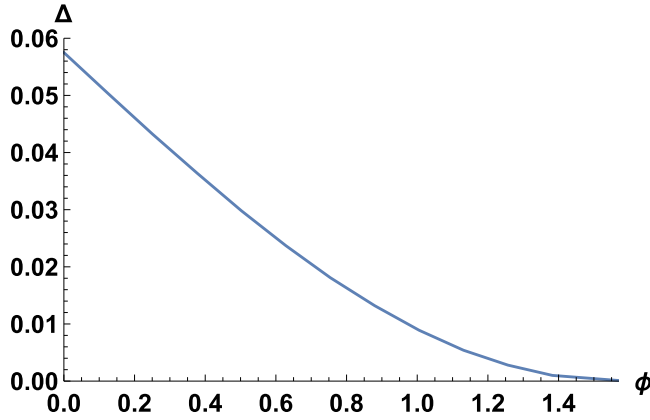


FIG. 4. The Berry phase for the CK model, where Δ vs ϕ is displayed. k, μ change along the trajectory on periodic environments with $k(t) = 1 + 0.025 \cos(t)$, $\mu(t) = 1 + 0.025 \sin(t + \phi)$. We consider a loop via a parameter $0 \leq t \leq 2\pi$. The loop contains a two-dimensional surface, which is maximal for $\phi = 0$ and minimal for $\phi = \pi/2$. Our numerics for $N = 2000$ gives Δ with the 10% accuracy.

$$W(x) = w(x) - \sqrt{w(x)^2 - (1 - x^2)},$$

$$dd(x) = -\sqrt{w(x)^2 - (1 - x^2)}. \quad (18)$$

Equations (16) and (17) give the $\delta\Delta$ for the small changes of δk and $\mu_2 - \mu_1$. In Fig. 4 we changed both fitness and mutation parameters k and μ around the cycles, getting Δ as an integral of $\delta\Delta$. The Berry phase disappears when both k and μ oscillate with the same phase.

It is possible to obtain a phase transition from one branch of the solution $f_1(s) = R_1$ to the other one, as described in Fig. 2(b). In this case there is a phase transition via the surplus, while the mean fitness is unchanged [30]. Figure 3(a) illustrates that the global Berry phase along the closed loop diverges near the phase transition point.

C. The calculation of the fluxes

Let us consider the change of two parameters of the model along the loop of integration in Eq. (1). We derived the Berry phase expression when both the mutation rates and fitnesses are changed along the path. We represent Eq. (14) as

$$\delta\Delta = A_1 dk_1 + A_2 dk_2,$$

$$F_{12} = \frac{dA_1}{dk_2} - \frac{dA_2}{dk_1}. \quad (19)$$

The Berry phase along the small loop is equal to $F_{12} \times dk_1 \times dk_2$.

Let us prove that when we change the parameters of the fitness along the closed loop then we get zero total Berry phase. If both parameters belong to the fitness function, then we denote them as k_1, k_2 , i.e., $f(x) = k_1 x + k_2 x^2/2$, and consider Eq. (13) for $\delta f = f'_1 \delta k_1 + f'_2 \delta k_2$, $f_x = f'_2 = x^2/2$. Then $F_{12} \sim f''_{12} - f''_{21} = 0$. The Berry phase along a closed loop equals mF_{12} times the surface constrained by the close loop. As we get that $F = 0$, Eq. (1) gives zero. We verified that there is a nonzero Berry phase also in case of the change of both mutation rates, forward and backward.

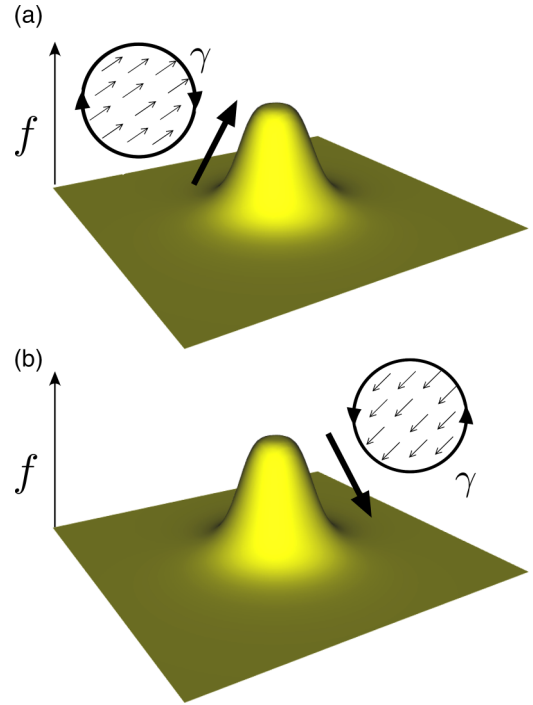


FIG. 5. Two schematic cases for the evolving population climbing the Wrightian peak on fitness landscape. The closed loops indicate two possible directions in the integration of Δ . In (a) the Berry phase allows the system to climb up, whereas in (b) it leads to a fitness reduction.

V. DISCUSSION

We derived an analytical expression for the Berry phase in evolution. The integral Δ can be understood as a measure of evolutionary hysteresis: it indicates whether the population gains or loses fitness over a cycle, which in turn reflects the presence of nonequilibrium forces and evolutionary irreversibility. In analogy to thermodynamic cycles, a nonzero Δ implies that the system does not return to the same effective state after a cyclic process, much as a system with dissipation [Figs. 5(a) and 5(b)]. The presence and impact of geometric phases in stochastic thermodynamics and evolutionary dynamics is a hot topic of modern statistical physics. While several approximate solutions have been derived for systems with few degrees of freedom as well as some general, simple analytical results regarding symmetric mutation rates, no equivalent results have been obtained so far for the geometric phase. Here, by solving the mutationally asymmetric Crow-Kimura model, we derived analytical results for the relaxation dynamic of changing fitness landscapes and the Berry phase. One particularly important result involves the conditions at a nonzero global phase, where it is important to change the parameters related to the “noncommutable” evolution forces. In Ref. [3] the Crow-Kimura model has been mapped exactly to the quantum Hamiltonian of Ising spins in imaginary time. The mutation and selection in that Hamiltonian are operators, which do not commute, and it is the same story with the backward and forward evolution forces. The Berry phase is zero when, along the loop, we change two different parameters of

the fitness. We can also consider other scenarios, changing both the mutation rate and fitness, forward or backward mutation rates, fitness and recombination, or both the mutation and recombination rates. In all these cases, we find a nonzero global Berry phase. In a considered case with a bulk transition (the mean fitness has another analytical expression after the transition point) the Berry phase diverges at a phase transition point while it is discontinuous in the case of a soft transition in the evolution models (the mean fitness is an analytic function at the transition point, while for some order parameter, the surplus is discontinuous), and there is a discontinuity in the Berry phase as well, such as the one in the quantum phase transition case [31].

We should further clarify the role of the Berry phase in evolution, looking the other evolution forces: insertion, deletion, duplication, and the carrying capacity (the dilution of the system to have a constant or restricted population size). Our results have certainly an impact on the growing complexity as well. We need a simultaneous change of parameters, not only the fitness landscape alone, to get a nontrivial situation, i.e., growing complexity [32,33].

Next, we should carefully define the phase in the stochastic processes in the case of detailed balance breaking [34,35], which is a typical situation in biological processes with a nonzero flux of an abstract magnetic field created by the monopole [36]. If the detailed balance is violated in different subsystems of the system accompanied with the Berry phases, the resonance in the Berry phases means simply similar F_{12} -es in the case of changing environments, i.e., small oscillations (biological sythms).

One relevant problem where the ideas presented here can help concerns origins of life scenarios where a periodic

input of energy and matter from the environment is at work. Such a scenario has been put forward in terms of wet-dry cycles affecting a given area where some organic soup would be present [37]. As a consequence of this periodic driving, molecules with increasing complexity could have been produced. Such drying and rewetting cycles would have happened in hydrothermal fields and helped the formation of complex molecules [38]. Since models of chemical reactions networks have been put forward to explain the impact of such periodic changes on evolving prebiotic systems, our framework could be helpful to define the conditions for such growth in complexity to occur. In particular, it could be useful to analyze previous models of polymerisation under wet-dry periodic cycling where polymer complexity is shown to emerge [39].

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DATA AVAILABILITY

The data are not publicly available. The data are available from the authors upon reasonable request.

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