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Self-similar potentials in random media, fractal evolutionary landscapes and Kimura's neutral theory of molecular evolution

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Abstract

A general method for constructing self-similar scalar fractal random fields is suggested based on the assumption that the fields are generated by a broad distribution of punctual sources. The method is illustrated by a problem of population biology, the evolution on a random fitness landscape. A random fitness landscape is constructed based on the following hypotheses. The landscape is defined by the dependence of a fitness variable ϕ on the state vector x of the individuals: $\phi = \phi(x)$; the corresponding hypersurface has a large number of local maxima characterized by a local probability law with variable parameters. These maxima are uniformly randomly distributed throughout the state space of the individuals. From generation to generation the heights and the shapes of these local maxima can change; this change is described in terms of two probabilities p and α that an individual modification occurs and that the process of variation as a whole stops, respectively. A general method for computing the stochastic properties of the evolutionary landscape is suggested based on the use of characteristic functionals. An explicit computation of the Fourier spectrum of the cumulants of the evolutionary landscape is performed in a limit of the thermodynamic type for which the number of maxima and the volume of the state space of the individuals tend to infinity but the density of maxima remains constant. It is shown that, although a typical realization of the evolutionary landscape is very rough, its average properties expressed by the Fourier spectrum of its cumulants are smooth and characterized by scaling laws of the power law type. The average landscape which is made up of the frozen contributions of the changes corresponding to different generations is flat, a result which is consistent with the Kimura's theory of molecular

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evolution. Some general implications of the suggested approach for the statistical physics of systems with random ultrametric topology are also investigated.

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1. Introduction

The study of transport processes in random media with static or dynamical disorder is a problem of topical interest in condensed matter physics [1–4]. In this context the concept of a random surface in real space or of a random hypersurface in an abstract space naturally emerges. For instance a random surface in real space may represent the border between two phases in a random medium. In other cases a random hypersurface in an abstract space can be used for representing a force potential in a random medium with static or dynamical disorder. Among the different types of random surfaces the ones displaying stochastic self-similar features play a central role in the physics of disordered systems. Such surfaces may display geometrical or statistical scale invariant features characteristic for fractal systems. Both the theoretical description and the experimental evaluation of the properties of such fractal random surfaces are difficult problems [5]. In this field exactly solvable models which are however complicated enough to be physically interesting are rare and the enriching of the collection of such models is most welcome.

The purpose of the present article is to suggest a simple exactly solvable model of a random self-similar surface which displays statistical-fractal features. Although inspired by a biological model, Kimura's theory of neutral molecular evolution [6–8], this model can be used both for physical and biological applications. Our procedure for generating fractal random surfaces could be presented in an abstract way, without reference to any application; however we prefer to present it in the biological context which has inspired it in the first place.

Kimura's theory of molecular evolution is a controversial topic of population genetics. This theory assumes that at a molecular level most mutations are neutral and that the fixation of most alleles of a gene within a population is purely a random effect. Although certain data of molecular biology support this theory it is not unanimously accepted by all scientists. One objection against Kimura's theory is that it corresponds to an almost flat fitness landscape which contradicts the observations supporting the existence of a very rough landscape [9]. Another contradiction is that Kimura's theory predicts a uniform rate of substitution of nucleotides (or of the corresponding aminoacids) during the evolution process whereas the observed substitution rate is not always uniform [10, 11]. A possible explanation of these contradictions is that what it is actually observed in only one realization of a random process whereas the flatness of the fitness landscape or the uniformity of the rate of substitution have a statistical nature and can be evaluated only by removing the random fluctuations by

means of an ensemble average. Such an explanation has been suggested in connection with the nonuniformity of the rate of substitution of nucleotides [10, 11].

Our suggestion is that this explanation can be extended to the case of the fitness landscape. We assume that the fitness landscape is random and is changing during the evolution process. The modifications of the landscape occur generation by generation. The random landscape which eventually emerges during the evolution process is made up of the “frozen” contributions of the changes occurring for different generations; in the language used in condensed matter physics [1–4] this situation would correspond to static disorder. These assumptions lead to a simple model for the evolutionary landscape which is amenable to complete analytical treatment; the results are of interest both for physics and biology.

The plan of the paper is as follows. In Section 2 we suggest a general approach for constructing self-similar scalar random fields with statistical fractal features by using the method of characteristic functionals. In Section 3 a Fourier analysis of the cumulants of the scalar random field is performed and the main statistical fractal features of the evolutionary landscape are investigated. In Sections 4 and 5 the implications of the model are discussed in connection with the possible biological and physical applications, respectively. Finally in Section 6 some open problems and possibilities of generalization of the suggested approach are analyzed.

2. Characteristic functionals and scalar fractal fields

We assume that an individual is characterized by a d_s -dimensional state vector

$$\mathbf{x} = (x_1, \dots, x_{d_s}). \quad (1)$$

which expresses the anatomical, biochemical, cytochemical and physiological state of the organism. Our purpose is to evaluate the fitness variable of a group of individuals characterized by a given state vector. Usually the fitness variable is expressed by the intrinsic rate of growth $r(\mathbf{x})$ of a homogeneous group of individuals characterized by the same state vector:

$$r = r(\mathbf{x}). \quad (2)$$

We assume that a realization of the hypersurface $r = r(\mathbf{x})$ has a large number of maxima of different sizes and shapes varying from very sharp and high to very wide and low and that these maxima are randomly and uniformly distributed in a given large region Σ of the \mathbf{x} -space. Although the widths and heights of the local maxima are different we assume that they are all generated by a multiple convolution of the same probability density of the displacement vector $\Delta\mathbf{x} = \mathbf{x} - \mathbf{x}_i$:

$$\varphi(\Delta\mathbf{x})d\Delta\mathbf{x}, \quad \int \varphi(\Delta\mathbf{x})d\Delta\mathbf{x} = 1, \quad (3)$$

where x_l is the position vector of a local maximum, x is the current position vector of a point on the landscape and Δx is the displacement vector of a current point on the landscape from the position of a maximum.

We assume that each evolutionary change can be represented by a convolution of the probability density $\varphi(\Delta x)$ with itself. If a local maximum is subject to n evolutionary changes then its contribution to the fitness landscape is proportional to

$$\underbrace{\varphi(\Delta x) \otimes \dots \otimes \varphi(\Delta x)}_{n \text{ times}} = [\varphi(\Delta x) \otimes]^{(n)}, \tag{4}$$

where \otimes denotes the convolution product in the x -space, that is, given two arbitrary functions of x , $f(x)$ and $g(x)$, we have

$$f(x) \otimes g(x) = \int f(x')g(x - x')dx'. \tag{5}$$

Denoting by

$$\xi(n|q), \sum_n \xi(n|q) = 1, \tag{6}$$

the probability that n evolutionary changes of a maximum take place in q generations, at the q th generation the contribution of a maximum to the evolutionary landscape is proportional to

$$\varphi_q(\Delta x) = \sum_n \xi(n|q) [\varphi(\Delta x) \otimes]^{(n)}. \tag{7}$$

The value of the fitness landscape for a given position x is made up, up to a constant proportionality factor, from the additive contributions of all the local maxima present in the region Σ of the x -space. If there are N local maxima placed at positions x_1, \dots, x_N , respectively, for which the evolutionary changes have occurred for q_1, \dots, q_N generations, respectively, we have

$$r(x) = v \phi(x), \tag{8}$$

where

$$\phi(x) = \sum_{l=1}^N \varphi_{q_l}(x - x_l) \tag{9}$$

is a non-normalized fitness variable and v is a constant proportionality factor with dimension

$$[v] = [x_1] [x_2] \dots /[\text{Time}]. \tag{10}$$

Since the local maxima are supposed to be uniformly and randomly distributed within the domain Σ , the probability

$$P(x)dx, \int_{\Sigma} P(x)dx = 1, \tag{11}$$

that the position of a maximum is between x and $x + dx$ is simply given by

$$P(x)dx = dx/V_{\Sigma}, \tag{12}$$

where

$$V_{\Sigma} = \int_{\Sigma} dx \tag{13}$$

is the volume of the domain Σ . We emphasize that the assumption of statistical independence of the positions of the different local maxima is introduced only in order to simplify the computations; the theory can be easily extended to the more general case when the positions of the maxima are correlated random variables described by a stochastic point process (see Appendix A).

Similarly the total number N of local maxima enclosed within the domain Σ is assumed to be a random variable selected from a certain probability distribution

$$B(N), \quad \sum_N B(N) = 1. \tag{14}$$

In this paper we do not assume an explicit form for the probability $B(N)$ of the number N of maxima. The only assumption made is that we have a summary knowledge of the nature of the fluctuations of the number of maxima. A similar approach has been suggested by two of the present authors in a different biological context, the propagation of space-dependent epidemics [12]. We define the characteristic function of the probability $B(N)$ as a discrete Fourier transform

$$G(b) = \sum_N \exp(i b N) B(N), \tag{15}$$

where b is the Fourier variable conjugate to the number N of local maxima. The cumulants $\langle\langle N^m \rangle\rangle$ of the number of local maxima are given by a Taylor expansion of the logarithm of the characteristic function $G(b)$:

$$\ln G(b) = \sum_{m=1}^{\infty} \frac{(i)^m}{m!} b^m \langle\langle N^m \rangle\rangle, \tag{16}$$

that is

$$\langle\langle N^m \rangle\rangle = (-i)^m \partial^m G(0)/\partial b^m. \tag{17}$$

In terms of these cumulants we introduce the relative fluctuations of different orders

$$c_m = \langle\langle N^m \rangle\rangle / \langle N \rangle^m, \quad m = 2, 3, \dots, \tag{18}$$

where

$$\langle\langle N \rangle\rangle = \langle N \rangle, \tag{19}$$

is the first cumulant of the number of maxima which, according to the definitions (16, 17) of the cumulants, is the same as the average value of the number of maxima.

If for large values of the average number of maxima $\langle N \rangle = \langle\langle N \rangle\rangle$, the relative fluctuations c_m , $m = 2, 3, \dots$ tend to zero

$$c_m \rightarrow 0 \quad m \geq 2, \quad \text{as } \langle N \rangle \rightarrow \infty, \quad (20)$$

then the fluctuations of the number of maxima are non-intermittent; otherwise if as $\langle N \rangle \rightarrow \infty$ the relative fluctuations of different orders do not decrease to zero but tend towards constant values different from zero or diverge to infinity then the fluctuations are intermittent. In this paper we assume the non-intermittency of the fluctuations of the number of maxima without making any particular assumption concerning the form of the probability $B(N)$, of the characteristic function $G(b)$ or the values of the cumulants $\langle\langle N^m \rangle\rangle$. This non-intermittency condition expresses in a quantitative way the fact that the fluctuations of the number of maxima are small in the limit of large domains Σ . Although not used explicitly in the case of biological application considered here, the study of intermittent fluctuations is of physical interest and it is presented shortly in Appendix B.

Concerning the stochastic properties of the number n of evolutionary changes of a maximum occurring in q generations we assume that for each generation there is a constant probability p that a change may occur. By analogy with an approach used in the theory of epidemic processes described by cellular automata [13], we can evaluate the probability of occurrence of a change in q generations as

$$\lambda(q) = 1 - (1 - p)^q. \quad (21)$$

Eq. (21) expresses the probability that a change occurs at least for one generation, $1 - p$ is the probability that no change occurs for a generation, $(1 - p)^q$ is the probability that no change occurs in all q generations and the complementary probability $1 - (1 - p)^q$ gives $\lambda(q)$. The probability $\xi(n|q)$ of occurrence of n changes in q generations is completely determined by the probability $\lambda(q)$ of the occurrence of a change in q generations; $\xi(n|q)$ is given by a Pascal law determined by $\lambda(q)$:

$$\xi(n|q) = [1 - \lambda(q)] [\lambda(q)]^{n-1} = (1 - p)^q [1 - (1 - p)^q]^{n-1}. \quad (22)$$

At q th generation the contribution of a maximum to the evolutionary landscape is given by (see Eq. (7)):

$$\varphi_q(\Delta \mathbf{x}) = (1 - p)^q \sum_{n=1}^{\infty} [\varphi(\Delta \mathbf{x}) \otimes]^{(n)} [1 - (1 - p)^q]^{n-1}. \quad (23)$$

By introducing the Fourier transform of $\varphi_q(\Delta \mathbf{x})$:

$$\bar{\varphi}_q(\mathbf{k}) = \int \exp(i \mathbf{k} \cdot \Delta \mathbf{x}) \varphi_q(\Delta \mathbf{x}) d\Delta \mathbf{x}, \quad (24)$$

where the overbar denotes the Fourier transformation and \mathbf{k} is the wave vector conjugate to the displacement vector $\Delta\mathbf{x}$, we come to

$$\bar{\varphi}_q(\mathbf{k}) = \frac{(1-p)^q}{[1 - \bar{\varphi}(\mathbf{k})]/\bar{\varphi}(\mathbf{k}) + (1-p)^q}, \tag{25}$$

where

$$\bar{\varphi}(\mathbf{k}) = \int \exp(i\mathbf{k} \cdot \Delta\mathbf{x}) \varphi(\Delta\mathbf{x}) d\Delta\mathbf{x}, \tag{26}$$

is the Fourier transform of the probability density $\varphi(\Delta\mathbf{x})$. The contribution $\varphi_q(\Delta\mathbf{x})$ to the fitness landscape can be computed from Eq. (25) by means of an inverse Fourier transformation

$$\begin{aligned} \varphi_q(\Delta\mathbf{x}) &= (2\pi)^{-d} \int \exp(-i\mathbf{k} \cdot \Delta\mathbf{x}) \\ &\times \frac{(1-p)^q}{[1 - \bar{\varphi}(\mathbf{k})]/\bar{\varphi}(\mathbf{k}) + (1-p)^q} d\mathbf{k}. \end{aligned} \tag{27}$$

The stochastic properties of the number q of generations for which a maximum is subject to the process of evolutionary change can be evaluated by assuming that for each generation there is a constant probability α that the process of evolutionary change as a whole does not take place. The probability $\chi(q)$ that the process of evolutionary change as a whole acts over q generations is given by a Pascal law similar to Eq. (22):

$$\chi(q) = \alpha(1-\alpha)^q. \tag{28}$$

By using a method borrowed from the theory of colored noise [14, 15] we describe the stochastic properties of the evolutionary landscape by means of the characteristic functional

$$Z[K(\mathbf{x})] = \left\langle \exp\left(i \int \phi(\mathbf{x}) K(\mathbf{x}) d\mathbf{x}\right) \right\rangle, \tag{29}$$

where $K(\mathbf{x})$ is a suitable test function and the average $\langle \dots \rangle$ is taken over all possible values N and $\mathbf{x}'_1, \dots, \mathbf{x}'_N$ of the number and positions of the maxima as well as over all the numbers of generations q_1, \dots, q_N during which the evolutionary changes take place. By inserting Eq.(9) into Eq.(29) and expressing the average explicitly we obtain

$$\begin{aligned} Z[K(\mathbf{x})] &= \sum_{N=0}^{\infty} \sum_{q_1=0}^{\infty} \dots \sum_{q_N=0}^{\infty} \int \dots \int B(N)\chi(q_1)\dots\chi(q_N)P(\mathbf{x}'_1) d\mathbf{x}'_1 \\ &\dots P(\mathbf{x}'_N) d\mathbf{x}'_N \exp\left(i \sum_{i=1}^N \int K(\mathbf{x})\varphi_{q_i}(\mathbf{x} - \mathbf{x}'_i) d\mathbf{x}\right) \\ &= G \left\{ b = -i \ln \left[\sum_{q=0}^{\infty} \chi(q) \right. \right. \\ &\quad \left. \left. \times \int \frac{d\mathbf{x}'}{V_Z} \left[\exp\left(i \int K(\mathbf{x})\varphi_q(\mathbf{x} - \mathbf{x}') d\mathbf{x}\right) - 1 \right] + 1 \right] \right\}, \end{aligned} \tag{30}$$

from which, by using the cumulant expansion (16) and expressing the cumulants $\langle\langle N^m \rangle\rangle$ in terms of the relative fluctuations c_m , $m = 2, 3, \dots$ given by Eq. (18) we come to

$$Z[K(\mathbf{x})] = \exp \left\{ \sum_{m=1}^{\infty} \frac{c_m}{m!} \varepsilon^m \left\{ V_{\Sigma} \ln \left[\frac{1}{V_{\Sigma}} \sum_{q=0}^{\infty} \alpha(1-\alpha)^q \int d\mathbf{x}' \right. \right. \right. \\ \left. \left. \left. \times \left[\exp \left[i \int K(\mathbf{x}) \varphi_q(\mathbf{x} - \mathbf{x}') d\mathbf{x} \right] - 1 \right] + 1 \right] \right\}^m \right\}, \quad (31)$$

where

$$\varepsilon = \langle N \rangle / V_{\Sigma}, \quad (32)$$

is the average volume density of maxima.

Now we introduce a limit of the thermodynamic type for which both the average number of maxima $\langle N \rangle$ and the volume V_{Σ} available in the \mathbf{x} -space tend to infinity but the average density of maxima remains constant,

$$V_{\Sigma}, \langle N \rangle \rightarrow \infty, \quad \varepsilon = \langle N \rangle / V_{\Sigma} = \text{constant}. \quad (33)$$

For non-intermittent fluctuations obeying the condition (20) in the thermodynamic limit (33), the expansion (31) for the characteristic functional of the evolutionary landscape tends towards a universal form which is independent of the details of the fluctuations of the number of maxima:

$$Z[K(\mathbf{x})] = \exp \left\{ \varepsilon \sum_{q=0}^{\infty} \alpha(1-\alpha)^q \int d\mathbf{x}' \left[\exp \left(i \int K(\mathbf{x}) \varphi_q(\mathbf{x} - \mathbf{x}') d\mathbf{x} \right) - 1 \right] \right\}. \quad (34)$$

A similar universal law is derived for intermittent fluctuations in Appendix B.

3. Fourier analysis of evolutionary landscape

The universal limit law (34) for non-intermittent fluctuations contains all stochastic information necessary for the characterization of the evolutionary landscape. By expressing the characteristic functional $Z[K(\mathbf{x})]$ in a cumulant expansion we get

$$Z[K(\mathbf{x})] = \exp \left\{ \sum_{m=1}^{\infty} \frac{(i)^m}{m!} \int \dots \int \langle\langle \phi(\mathbf{x}_1) \dots \phi(\mathbf{x}_m) \rangle\rangle K(\mathbf{x}_1) \dots K(\mathbf{x}_m) d\mathbf{x}_1 \dots d\mathbf{x}_m \right\}, \quad (35)$$

and thus the cumulants of the non-normalized fitness function $\phi(\mathbf{x})$ are given by the functional derivatives

$$\langle\langle \phi(\mathbf{x}_1) \dots \phi(\mathbf{x}_m) \rangle\rangle = (-i)^m \frac{\delta^m \ln Z[K(\mathbf{x})]}{\delta K(\mathbf{x}_1) \dots \delta K(\mathbf{x}_m)} \Big|_{K(\mathbf{x})=0}. \quad (36)$$

By inserting Eq.(34) into Eq.(36) and evaluating the functional derivatives of the logarithm of the characteristic functional with respect to $K(x_1), \dots, K(x_m)$ we obtain

$$\langle\langle \phi(x_1) \cdots \phi(x_m) \rangle\rangle = \sum_{q=0}^{\infty} \alpha(1-\alpha)^q \int \varphi_q(x_1-x') \cdots \varphi_q(x_m-x') dx'. \tag{37}$$

Now we perform a Fourier analysis of the cumulants of the fitness landscape. The Fourier spectrum of the cumulant of the m th order is given by:

$$\langle\langle \bar{\phi}(k_1) \cdots \bar{\phi}(k_m) \rangle\rangle = \int \cdots \int \exp\left(i \sum_{u=1}^m x_u \cdot k_u\right) \langle\langle \phi(x_1) \cdots \phi(x_m) \rangle\rangle dx_1 \cdots dx_m. \tag{38}$$

By inserting Eqs.(25) and (37) into Eq.(38) and using the Fourier representation of the delta function,

$$\delta(k) = (2\pi)^{-d} \int \exp(i x \cdot k) dx, \tag{39}$$

we get

$$\langle\langle \bar{\phi}(k_1) \cdots \bar{\phi}(k_m) \rangle\rangle = (2\pi)^d \delta\left(\sum_{u=1}^m k_u\right) S_m(k_1, \dots, k_m), \tag{40}$$

$$S_m(k_1, \dots, k_m) = \varepsilon \alpha \sum_{q=0}^{\infty} (1-\alpha)^q \prod_{u=1}^m \left(\frac{(1-p)^q}{[1-\bar{\varphi}(k_u)]/\bar{\varphi}(k_u) + (1-p)^q} \right). \tag{41}$$

The structure of the Fourier spectrum of the cumulants outlines that the evolutionary landscape is statistically translationally invariant. Indeed, due to the delta function factor $\delta(\Sigma k_u)$ in Eq.(40) the inverse Fourier transform

$$\begin{aligned} \langle\langle \phi(x_1) \cdots \phi(x_m) \rangle\rangle &= (2\pi)^{-d} \int \cdots \int \exp\left(-i \sum_{u=1}^m x_u \cdot k_u\right) \\ &\quad \times \langle\langle \bar{\phi}(k_1) \cdots \bar{\phi}(k_m) \rangle\rangle dk_1, \dots, dk_m \\ &= \int \cdots \int \delta\left(\sum_{u=1}^m k_u\right) \exp\left(-i \sum_{u=1}^m x_u \cdot k_u\right) \\ &\quad \times S_m(k_1, \dots, k_m) dk_1 \cdots dk_m \end{aligned} \tag{42}$$

obeys the condition

$$\langle\langle \phi(x_1) \cdots \phi(x_m) \rangle\rangle = \langle\langle \phi(x_1 - \Delta x) \cdots \phi(x_m - \Delta x) \rangle\rangle, \quad \Delta x = \text{arbitrary}, \tag{43}$$

which expresses the condition of statistical translational invariance with respect to an arbitrary displacement vector Δx . Eq.(43) can be proven by expressing both its terms as inverse Fourier transforms and noticing that

$$\delta\left(\sum_{u=1}^m k_u\right) \exp\left(i \Delta x \cdot \sum_{u=1}^m k_u\right) = \delta\left(\sum_{u=1}^m k_u\right). \tag{44}$$

For investigating the possible self-similar features of the Fourier spectrum of the cumulants we evaluate in Eq.(41) the sum over the number q of generations by means of the Poisson summation formula [16]. We have

$$\begin{aligned}
 S_m(\mathbf{k}_1, \dots, \mathbf{k}_m) &= \frac{\alpha\varepsilon}{2} \prod_{u=1}^m \left(\frac{\bar{\varphi}(\mathbf{k}_u)}{1 - \bar{\varphi}(\mathbf{k}_u)} \right) \\
 &+ \frac{\alpha\varepsilon}{-\ln(1-p)} \int_0^1 dy y^{H+m-1} \prod_{u=1}^m \left[y + \frac{1 - \bar{\varphi}(\mathbf{k}_u)}{\bar{\varphi}(\mathbf{k}_u)} \right]^{-1} \\
 &+ \frac{2\alpha\varepsilon}{-\ln(1-p)} \sum_{v=1}^{\infty} \int_0^1 dy y^{H+m-1} \prod_{u=1}^m \left[y + \frac{1 - \bar{\varphi}(\mathbf{k}_u)}{\bar{\varphi}(\mathbf{k}_u)} \right]^{-1} \\
 &\times \cos\left(\frac{2\pi v \ln y}{-\ln(1-p)} \right), \tag{45}
 \end{aligned}$$

where

$$H = [\ln(1 - \alpha)]/[\ln(1 - p)], \tag{46}$$

is a positive fractal exponent which characterizes the competition between the probability $1 - p$ that an individual change does not take place and the probability $1-\alpha$ that the process of changing as a whole takes place.

Eq.(45) displays some typical features of the solution of a renormalization group equation [17, 18] and thus we expect it to generate a scaling law of the negative power law type modulated by logarithmic oscillations of the wave vector. To avoid the complications generated by the logarithmic oscillations we consider a special limit in which the power law scaling is still present but the logarithmic oscillations disappear [19]. We assume that

$$\alpha, p \searrow 0, \quad H = \text{constant}. \tag{47}$$

In this limit Eq.(45) becomes

$$S_m(\mathbf{k}_1, \dots, \mathbf{k}_m) = \varepsilon H \int_0^1 dy y^{H+m-1} \prod_{u=1}^m \left(y + \frac{1 - \bar{\varphi}(\mathbf{k}_u)}{\bar{\varphi}(\mathbf{k}_u)} \right)^{-1}. \tag{48}$$

For simplicity we evaluate only the Fourier spectrum of the cumulants of first and second order. For $m = 1$ we have

$$S_1(\mathbf{k}) = \varepsilon, \tag{49}$$

which corresponds to a completely flat average evolutionary landscape, as required by Kimura’s theory of molecular evolution [6–8]:

$$\langle\langle \phi(\mathbf{x}) \rangle\rangle = (2\pi)^{-d} \int \langle\langle \bar{\varphi}(\mathbf{k}) \rangle\rangle \exp(-i\mathbf{x} \cdot \mathbf{k}) d\mathbf{k} = \varepsilon. \tag{50}$$

It is easy to check that this result is valid even for $\alpha, p \neq 0$ when the logarithmic oscillations are present.

For evaluating the spectrum of the cumulants of the second order we limit ourselves to the case of unimodal and symmetric probability densities $\varphi(\Delta \mathbf{x}) d\Delta \mathbf{p}$ for which the average value $\langle \Delta \mathbf{x} \rangle$ of the displacement vector is equal to the most probable value $\Delta \mathbf{x}_p = \mathbf{0}$:

$$\langle \Delta \mathbf{x} \rangle = \int \Delta \mathbf{x} \varphi(\Delta \mathbf{x}) d\Delta \mathbf{x} = \Delta \mathbf{x}_p = \mathbf{0}. \tag{51}$$

Note that, if this property is initially valid, it is conserved during the evolution process because the average value corresponding to a multiple convolution product of probability densities is the sum of the individual average values. We distinguish two cases.

(1) If the cumulants of the second order of the components of the displacement vector exist and are finite

$$\langle \langle \Delta x_u \Delta x_u \rangle \rangle = \langle \Delta x_u \Delta x_u \rangle = \text{finite}, \tag{52}$$

then through a suitable linear transformation of the coordinate system in the \mathbf{x} -state space we can always make that the matrix $[\langle \langle \Delta x_u \Delta x_u \rangle \rangle]$ is diagonal, i.e.,

$$\langle \langle \Delta x_u \Delta x_u \rangle \rangle = \langle \langle \Delta x_u^2 \rangle \rangle \delta_{uu}, \tag{53}$$

and as $|\mathbf{k}| \rightarrow 0$ the Fourier transform of $\varphi(\Delta \mathbf{x})$, $\bar{\varphi}(\mathbf{k})$, can be represented as

$$\bar{\varphi}(\mathbf{k}) \sim 1 - \frac{1}{2} \sum_u \langle \langle \Delta x_u^2 \rangle \rangle k_u^2, \text{ as } |\mathbf{k}| \rightarrow 0. \tag{54}$$

(2) If the probability density of the displacement vector, $\varphi(\Delta \mathbf{x})$, has a long tail of the inverse power law type, then the cumulants $\langle \langle \Delta x_u^2 \rangle \rangle$ diverge and Eq.(54) is replaced by

$$\bar{\varphi}(\mathbf{k}) \sim 1 - [\sum c_u (k_u)^2]^\beta, \quad 1 > \beta > 0, \quad c_u \geq 0, \tag{55}$$

where β is a fractal exponent between zero and unity and c_u are constants.

In both cases in the limit $|\mathbf{k}| \rightarrow 0$ we have

$$\bar{\varphi}(\mathbf{k}) = \bar{\varphi}(-\mathbf{k}), \tag{56}$$

and thus we can represent the Fourier spectrum of the second cumulant of the landscape in the form:

$$\begin{aligned} \langle \langle \bar{\varphi}(\mathbf{k}_1) \bar{\varphi}(\mathbf{k}_2) \rangle \rangle &\sim (2\pi)^d \delta(\mathbf{k}_1 + \mathbf{k}_2) S_2(\mathbf{k}_1, -\mathbf{k}_1) \\ &= (2\pi)^d \delta(\mathbf{k}_1 + \mathbf{k}_2) S_2(\mathbf{k}_1, \mathbf{k}_1). \end{aligned} \tag{57}$$

We get

$$\begin{aligned} S_2(\mathbf{k}, \mathbf{k}) &= \varepsilon H \int_0^1 dy y^{H+1} [y + (1 - \bar{\varphi}(\mathbf{k}))/\bar{\varphi}(\mathbf{k})]^{-2} \\ &= \varepsilon + \varepsilon H \left[1 - \bar{\varphi}(\mathbf{k}) - (H + 1) \left(\frac{1 - \bar{\varphi}(\mathbf{k})}{\bar{\varphi}(\mathbf{k})} \right)^H B(H, 1 - H, \bar{\varphi}(\mathbf{k})) \right], \end{aligned} \tag{58}$$

where

$$B(p, q, x) = \int_0^x x^{p-1} (1-x)^{q-1} dx, \quad x \geq 0, \quad p, q > 0, \tag{59}$$

is the incomplete beta function.

Now we can compute the scaling laws for the Fourier spectrum in the limit of small wave vectors $|\mathbf{k}_1|, |\mathbf{k}_2| \rightarrow 0$. We obtain

(1) If $\bar{\varphi}(\mathbf{k})$ is given by Eq.(54) then

$$\begin{aligned} \langle\langle \bar{\varphi}(\mathbf{k}_1) \bar{\varphi}(\mathbf{k}_2) \rangle\rangle &\sim (2\pi)^d \varepsilon \delta(\mathbf{k}_1 + \mathbf{k}_2) \\ &\times \left[1 - \frac{\pi H(H+1)}{\sin(\pi H)} \left(\frac{1}{2} \sum_u \langle\langle \Delta x_u^2 \rangle\rangle (k_{1u})^2 \right)^H \right], \quad |\mathbf{k}_1|, |\mathbf{k}_2| \rightarrow 0. \end{aligned} \tag{60}$$

(2) If $\bar{\varphi}(\mathbf{k})$ is given by Eq.(55) then

$$\begin{aligned} \langle\langle \bar{\varphi}(\mathbf{k}_1) \bar{\varphi}(\mathbf{k}_2) \rangle\rangle &\sim (2\pi)^d \varepsilon \delta(\mathbf{k}_1 + \mathbf{k}_2) \\ &\times \left[1 - \frac{\pi H(H+1)}{\sin(\pi H)} \left(\sum_u c_u (k_{1u})^2 \right)^{\beta H} \right], \quad |\mathbf{k}_1|, |\mathbf{k}_2| \rightarrow 0. \end{aligned} \tag{61}$$

We note that in both cases the Fourier spectrum for small wave vectors, which in the x -space corresponds to large vectors, has a scaling behavior of the power law type which expresses the self-similar features of the fluctuations of the evolutionary landscape.

4. Biological implications

For outlining the differences between the average landscape, which is flat, and a given realization, which is typically extremely rough, we evaluate the shape of a maximum subject to the evolutionary changes for q generations. Up to a constant proportionality factor such a maximum is represented by the probability density $\varphi_q(\Delta x)$ of the displacement vector given by Eq.(27) or by its Fourier transform $\varphi_q(\mathbf{k})$ given by Eq.(25), which plays the role of a characteristic function.

The cumulants of the components of the displacement vector at q -th generation can be computed from the characteristic function $\bar{\varphi}_q(\mathbf{k})$ given by Eq.(25) by applying a relationship similar to Eqs.(17) or (36)

$$\langle\langle x_{u_1} \dots x_{u_m} \rangle\rangle(q) = (-i)^m \frac{\partial^m \bar{\varphi}_q(\mathbf{k} = \mathbf{0})}{\partial k_{u_1} \dots \partial k_{u_m}}, \tag{62}$$

which can be derived by direct differentiation of Eq.(26). By applying Eq.(62) for $m = 2$ and using the expression (25) for $\bar{\varphi}_q(\mathbf{k})$ after some calculus we get the following

exact expressions for the cumulants of the second order of the components of the displacement vector at q th generation:

$$\langle\langle \Delta x_{u_1}, \Delta x_{u_2} \rangle\rangle(q) = \mathcal{M}_{u_1, u_2} (1 - p)^{-q} = \mathcal{M}_{u_1, u_2} \exp(q/q_c), \tag{63}$$

where

$$\mathcal{M} = [\mathcal{M}_{u_1, u_2}] = [\langle\langle \Delta x_u, \Delta x_{u'} \rangle\rangle], \tag{64}$$

are the cumulants of the second order of the components of the displacement vector attached to the initial probability density $\varphi(\Delta \mathbf{x})$ of the displacement vector at 0th generation and

$$q_c = 1/[-\ln(1 - p)] > 0, \tag{65}$$

is a characteristic generation scale.

Eqs.(63) for the cumulants of the second order at the q -th generation are exact; they hold for any probability density $\varphi(\Delta \mathbf{x})$ with finite cumulants. A similar exact expression for the height of a maximum cannot be derived. An approximate expression can be derived by expanding the logarithm of the characteristic function $\bar{\varphi}_q(\mathbf{k})$ in a Taylor series in the limit $|\mathbf{k}| \rightarrow 0$ and by keeping the first non-vanishing term

$$\ln \bar{\varphi}_q(\mathbf{k}) = -\frac{1}{2} \mathbf{k}^+ \mathcal{M} \mathbf{k} (1 - p)^{-q} + O(|\mathbf{k}|^3) \quad \text{as } |\mathbf{k}| \rightarrow 0. \tag{66}$$

In this approximation the probability density $\varphi_q(\Delta \mathbf{x})$ of the displacement vector at q -th generation can be easily evaluated by means of an inverse Fourier transformation. By inserting Eq.(66) into Eqs.(25)–(27) and by evaluating the integrals over \mathbf{k} we get a multivariate Gaussian probability density:

$$\begin{aligned} \varphi_q(\Delta \mathbf{x}) &= (2\pi)^{-d_s/2} (\det \mathcal{M})^{-1/2} \exp(-d_s q/2 q_c) \\ &\times \exp[-\frac{1}{2} \Delta \mathbf{x}^+ \mathcal{M}^{-1} \Delta \mathbf{x} \exp(-q/q_c)]. \end{aligned} \tag{67}$$

According to Eq.(67) a maximum subject to the evolutionary change for q generations has the shape of a $(d_s + 1)$ -dimensional Gaussian bell. The height of the bell is decreasing exponentially with the number of generations

$$\varphi_q(0) = (2\pi)^{-d_s/2} (\det \mathcal{M})^{-1/2} \exp(-d_s q/2 q_c), \tag{68}$$

with a rate of decrease equal to

$$d_s/(2q_c) = -\frac{1}{2} d_s \ln(1 - p). \tag{69}$$

A horizontal section of the Gaussian bell is given by a d_s -dimensional ellipsoid. The magnitude order of the parameters of a typical ellipsoidal section can be determined by diagonalizing the matrix $\langle\langle \Delta x_u, \Delta x_{u'} \rangle\rangle(q)$. Note that, since according to Eq.(63) they can be derived from each other by multiplication with a scalar, both matrices $\langle\langle \Delta x_u, \Delta x_{u'} \rangle\rangle(q)$ and \mathcal{M} can be simultaneously diagonalized, resulting in

$$\langle\langle \Delta x_u^2 \rangle\rangle(q) = \langle\langle \Delta x_u^2 \rangle\rangle \exp(q/q_c). \tag{70}$$

According with a well known geometrical property the diagonal elements (70) give the linear dimensions of the principal axes of the ellipsoid; it follows that the typical width of the Gaussian bell increases exponentially with the number q of generations.

The above computations show that the evolutionary process leads to the flattening and to the broadening of a maximum and that this process is exponentially fast. Since the eventual evolutionary landscape is made up of the contributions of various periods q_1, q_2, \dots over which the change acts, a typical realization contains all kinds of maxima from very high and narrow (q small) to very low and broad (q large). Note that, according to Eq.(28) for $\chi(q)$, the contribution of very large successions of generations, which correspond to very large maxima, is exponentially rare and that most maxima are the result of a small number of evolutionary changes (q small) and are high and narrow. Even though very rare, the very low and broad maxima are enough for generating the flattening of the average landscape.

The type of landscape considered in this paper may serve as a basis for the reconciliation of the neutralist [6–8] and selectionist [20–22] views in population genetics. The evolution process which has occurred on Earth is unique; it corresponds to a single realization of a random process and, according to the ideas developed in this paper, the corresponding landscape should be very rough. The roughness of the landscape would lead to a selection pressure, which apparently would contradict the neutralist theory. However, the contradiction is only apparent, because the selection process is to a great extent spurious since the factors shaping the landscape are completely random. Since the fitness enters the evolution equations for the population in a multiplicative way (see Ref. [22] and Appendix C) we expect that the dynamics of the process described by the present model is more complex than the dynamics predicted by the pure selectionist or neutralist theories. The main difficulties related to such a description for the evolution of population density are outlined in Appendix C.

5. Physical implications

Although the construction of a self-similar scalar random field presented in this paper has been suggested by a problem of population genetics, it is also of interest in various physical contexts. Our approach provides a very simple model of a self-similar random surface for which a detailed analysis of the Fourier spectrum of the cumulants is possible. From the physical point of view it gives a simple representation of a system with static disorder which eventually emerges due to the independent modification of the different parts of the system.

The structure of a typical realization of the landscape, which contains a very broad distribution of maxima, closely resembles a structure with ultrametric topology [23–25]; such structures with ultrametric topology are very important in the physics of disordered systems. For outlining the connections between the model of landscape suggested in this paper and an ultrametric structure, we use the Gaussian approximation (66) for the characteristic function $\bar{\varphi}_q(\mathbf{k})$ for the evaluation of the Fourier

spectrum of the cumulants of the landscape. By inserting Eq.(66) into Eq.(41) for $S_m(\mathbf{k}_1, \dots, \mathbf{k}_m)$ we come to

$$S_m(\mathbf{k}_1, \dots, \mathbf{k}_m) = \varepsilon \alpha \sum_{Q=0}^{\infty} (1 - \alpha)^Q \times \exp[-\mathcal{R}_m(\mathbf{k}_1, \dots, \mathbf{k}_m)(1 - p)^{-Q}], \tag{71}$$

$$\mathcal{R}_m(\mathbf{k}_1, \dots, \mathbf{k}_m) = \frac{1}{2} \sum_{u=1}^m \mathbf{k}_u^+ \mathcal{M} \mathbf{k}_u. \tag{72}$$

Note that Eqs.(71), (72) lead to a simple approximation of the Fourier spectrum as $|\mathbf{k}| \rightarrow 0$. By evaluating the sum over the generation index q in Eq.(71) by means of the Poisson summation technique and passing to the continuous limit (47) we obtain

$$S_m(\mathbf{k}_1, \dots, \mathbf{k}_m) \sim \varepsilon \{ \exp[-\mathcal{R}_m(\mathbf{k}_1, \dots, \mathbf{k}_m)] - [\mathcal{R}_m(\mathbf{k}_1, \dots, \mathbf{k}_m)]^H \Gamma[1 - H, \mathcal{R}_m(\mathbf{k}_1, \dots, \mathbf{k}_m)] \}. \tag{73}$$

from which we get the following expression for the Fourier spectrum:

$$\langle\langle \bar{\phi}(\mathbf{k}_1) \dots \bar{\phi}(\mathbf{k}_m) \rangle\rangle \sim (2\pi)^d \varepsilon \{ 1 - \Gamma(1 - H) [\mathcal{R}_m(\mathbf{k}_1, \dots, \mathbf{k}_m)]^H \} \delta\left(\sum_u \mathbf{k}_u\right), \tag{74}$$

where

$$\Gamma(a, x) = \int_x^{\infty} t^{a-1} \exp(-t) dt, \quad a > 0, \quad x \geq 0, \tag{75}$$

is the complementary incomplete gamma function and $\Gamma(a) = \Gamma(a, 0)$ is the complete gamma function. Eq.(74) reproduces the same type of \mathbf{k} -dependence for the cumulant of the second order of the landscape, $\langle\langle \bar{\phi}(\mathbf{k}_1) \bar{\phi}(\mathbf{k}_2) \rangle\rangle$, as the exact asymptotic expression (60); the corresponding proportionality coefficients are however different.

From Eq.(71) the connection between our model of fractal landscape and the conventional structures with an ultrametric topology [23–25] is clear. Eq.(71) has a structure similar to a relaxation equation for a process with ultrametric topology, where the function $\mathcal{R}_m(\mathbf{k}_1, \dots, \mathbf{k}_m)$ is the analogue of dimensionless time. This type of structure is generated by the random alteration of the initial landscape, which occurs hierarchically, step by step, generation by generation, in perfect analogy with the relaxation on ultrametric spaces, which occurs in a hierarchical way, level by level. The evolutionary change of the landscape leads to a hierarchical structure of maxima, which can be organized in an ultrametric topology formed of different levels. The maxima subject to the same number of transformation steps have the same characteristics and belong to the same level of the ultrametric structure.

Our model leads to an additional complication related to the fluctuations of the number and positions of the maxima, features which are missing in the conventional models with ultrametric topology reported in the literature [23–25]. The possible

fractal structure of these fluctuations may lead to interesting interference phenomena with the main ultrametric structure of the model. Such a possibility is considered in Appendix B by assuming that the fluctuations of the number of maxima are intermittent and characterized by a fractal exponent \mathcal{H} . The characteristic functional of the landscape is (see Appendix B):

$$Z[K(\mathbf{x})] = \mathcal{J}_{\mathcal{H}} \left\{ \varepsilon \sum_{q=0}^{\infty} \chi(q) \int d\mathbf{x}' \left[1 - \exp \left(i \int K(\mathbf{x}) \varphi_q(\mathbf{x} - \mathbf{x}') d\mathbf{x} \right) \right] \right\}, \quad (76)$$

where the function $\mathcal{J}_{\mathcal{H}}(z)$ can be expressed in terms of the incomplete gamma function

$$\gamma(a, u) = \int_0^u t^{a-1} \exp(-t) dt, \quad a > 0, \quad u \geq 0. \quad (77)$$

We have

$$\mathcal{J}_{\mathcal{H}}(z) = \mathcal{H} [(1 + 1/\mathcal{H})z]^{-\mathcal{H}} \gamma[\mathcal{H}, (1 + 1/\mathcal{H})z]. \quad (78)$$

The fractal landscape corresponding to the characteristic functional (76) is much rougher than the landscape corresponding to non-intermittent fluctuations. We note that Eq.(76) is nonanalytic in the vicinity $K(\mathbf{x}) = 0$ and then all functional derivatives (36) are infinite and the cumulants of the landscape diverge. The effect due to the intermittent nature of the fluctuations, which leads to the nonanalyticity of the characteristic functional $Z[K(\mathbf{x})]$, is much stronger than the effect of the main ultrametric structure generated by the hierarchical modification of the maxima.

6. Discussion

The type of landscape introduced in this paper is a simple model for a system with static disorder displaying self-similar features. The self-similarity is generated by the competition between two opposite factors: the hierarchical modification of the maxima, characterized by the individual probability of occurrence p , and the possibility that for each step(generation) the process of change stops, characterized by the overall probability α . Due to the equilibration between these two opposite effects a broad distribution of maxima eventually emerges, ranging from the very sharp and high ones which are very frequent to the low and broad ones which are exponentially rare. This broad distribution generates the lack of a characteristic length scale of the maxima expressed in the power scaling laws of the Fourier spectrum. We point out a formal analogy between this mechanism of generating power laws and a new type of self-organized criticality with competition recently suggested by Kluiving et al. [26].

Further studies of the type of landscape introduced here are of interest both from the biological and physical points of view. In connection with the possible biological applications it is necessary to elaborate techniques for the study of the evolution process itself occurring on the type of landscape considered here. The stochastic

equations describing the evolution of a population on a fractal landscape, even in the simplest case of monoecious asexual populations, are much more complicated than the stochastic equations commonly used in population genetics. These equations describe the evolution of a population under the influence of multiplicative fractal noise which may generate some unexpected features such as the lack of self-averaging, breaking of ergodicity etc. Although these types of equations are of topical interest in statistical physics [1–4] they have been barely used in population biology [27–29].

From the physical point of view further studies of the self-similar features of the fluctuating landscapes are of interest, especially in the case of intermittent fluctuations described by the non-analytic characteristic functional (76). Other direction of research is related to possible applications, for instance the use of the landscape as a simple model of a fractal surface, the analysis of light scattering on such a surface, fitting the measured data for real surfaces [5] by adjusting the parameters of the model, etc. Another possible application of the random landscape is the description of the properties of a fluctuating medium.

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Appendix A

If the maxima of the evolutionary landscape are not independent then the stochastic properties of their number N and positions x_1, \dots, x_N can be described by using the theory of random point processes [30]. We introduce the grand canonical number-position joint probability density

$$Q_0, Q_N(x_1, \dots, x_N) dx_1, \dots, dx_N, \quad (\text{A.1})$$

with the normalization condition

$$Q_0 + \sum_{N=1}^{\infty} \int \dots \int \frac{1}{N!} Q_N(x_1, \dots, x_N) dx_1 \dots dx_N = 1, \quad (\text{A.2})$$

and the generating functional

$$\begin{aligned} A[W(x)] = Q_0 + \sum_{N=1}^{\infty} \frac{1}{N!} \int \dots \int Q_N(x_1, \dots, x_N) \\ \times W(x_1) \dots W(x_N) dx_1 \dots dx_N, \end{aligned} \quad (\text{A.3})$$

where $W(\mathbf{x})$ is a suitable test function. The expression (30) for the characteristic functional $Z(K(\mathbf{x}))$ becomes

$$Z(K(\mathbf{x})) = \Lambda \left[W(\mathbf{x}) = \sum_{q=0}^{\infty} \chi(q) \exp \left(i \int K(\mathbf{x}') \varphi_q(\mathbf{x}' - \mathbf{x}) d\mathbf{x}' \right) \right]. \quad (\text{A.4})$$

In particular if the maxima are independent we have

$$Q_0 = B(0), \quad Q_N(\mathbf{x}_1, \dots, \mathbf{x}_N) = N! B(N) P(\mathbf{x}_1) \cdots P(\mathbf{x}_N), \quad (\text{A.5})$$

and Eq.(A.4) reduces to Eq.(30) derived in Section 2.

Appendix B

For intermittent fluctuations a representation of the probability $\tilde{B}(N)$ of the number of maxima can be derived by applying a probabilistic version [31] of the Shlesinger–Hughes stochastic renormalization procedure [32]. The method consists in starting from an initial probability $B(N)$ for the number of maxima characteristic for non-intermittent fluctuations and in constructing from it a renormalized probability $\tilde{B}(N)$ for which the fluctuations are intermittent. A similar computation has been performed in Ref. [12] in the context of the theory of epidemics. To save space we do not present here the detailed computation for the determination of the renormalized probability $\tilde{B}(N)$. Here we give only the relationship between the characteristic function of the renormalized probability

$$\tilde{G}(b) = \sum_{N=0}^{\infty} \exp(ibN) \tilde{B}(N), \quad (\text{B.1})$$

and the non-renormalized characteristic function $G(b)$ of the probability $B(N)$, given by Eq.(15). We have [12]:

$$\tilde{G}(b) = \mathcal{H} \int_0^1 z^{\mathcal{H}-1} dz G(-i \ln \{1 - z[1 - \exp(ib)]\}), \quad 1 > \mathcal{H} > 0, \quad (\text{B.2})$$

where \mathcal{H} is a second fractal exponent between zero and unity which characterizes the intermittent behaviour of the fluctuations of the number of maxima.

In this case Eq.(30) for the characteristic functional $Z[K(\mathbf{x})]$ remains valid with the difference that the characteristic function $G(b)$ of the non-renormalized probability density $B(N)$ is replaced by the renormalized expression $\tilde{G}(b)$ given by Eq.(B.2). We get:

$$Z[K(\mathbf{x})] = \mathcal{H} \int_0^1 z^{\mathcal{H}-1} dz G \left\{ -i \ln \left\{ 1 + z \sum_{q=0}^{\infty} \chi(q) \int \frac{d\mathbf{x}'}{V_z} \right. \right. \\ \left. \left. \times \left[\exp \left(i \int K(\mathbf{x}) \varphi_q(\mathbf{x} - \mathbf{x}') d\mathbf{x} \right) - 1 \right] \right\} \right\}. \quad (\text{B.3})$$

We express the average renormalized number of maxima

$$\langle \tilde{N} \rangle = \sum_{N=0}^{\infty} N \tilde{B}(N) = -i \frac{\partial \tilde{G}(b=0)}{\partial b}, \tag{B.4}$$

in terms of the corresponding non-renormalized quantity

$$\langle N \rangle = \sum_{N=0}^{\infty} N B(N) = -i \frac{\partial G(b=0)}{\partial b}. \tag{B.5}$$

We get

$$\langle \tilde{N} \rangle = \langle N \rangle \mathcal{H} / (\mathcal{H} + 1). \tag{B.6}$$

For computing the universal law for the characteristic functional of the landscape $Z[K(x)]$ which emerges in the thermodynamic limit (33) we expand the non-renormalized characteristic function $G(b)$ in the cumulant series (16) and express the non-renormalized cumulants $\langle\langle N^m \rangle\rangle$ in terms of the non-renormalized relative fluctuations c_m given by Eqs.(18) and in terms of the average renormalized density of maxima

$$\varepsilon = \frac{\langle \tilde{N} \rangle}{V_{\Sigma}} = \frac{\mathcal{H}}{\mathcal{H} + 1} \frac{\langle N \rangle}{V_{\Sigma}}. \tag{B.7}$$

We obtain

$$\begin{aligned} Z[K(x)] &= \mathcal{H} \int_0^1 z^{\mathcal{H}-1} dz \exp \left\{ \sum_{m=1}^{\infty} \frac{c_m}{m!} [\varepsilon(1 + 1/\mathcal{H})]^m \right. \\ &\quad \times \left. \left\{ V_{\Sigma} \ln \left[1 + z \sum_{q=0}^{\infty} \chi(q) \int \frac{d\mathbf{x}'}{V_{\Sigma}} \right. \right. \right. \\ &\quad \left. \left. \left. \times \left[\exp \left(i \int K(x) \varphi_q(\mathbf{x} - \mathbf{x}') d\mathbf{x} \right) - 1 \right] \right\} \right\}^m \right\}. \tag{B.8} \end{aligned}$$

By passing in Eq.(B.8) to the thermodynamic limit (33) and using the non-intermittency conditions (20) for the non-renormalized probability $B(N)$ we get the universal law (76) for the characteristic functional $Z[K(x)]$.

Appendix C

In this appendix we present an attempt to reconcile the selectionist evolution theories of the Fisher–Eigen type [20–22] with Kimura’s theory of neutral evolution [6–8] for the simplest case of monoecious asexual populations. We assume the validity of two simplifying assumptions. (1) The random evolutionary landscape is

shaped in the initial stages of the evolutionary process; in the late stages of the evolution process considered here the random evolutionary landscape is constant and made up of the frozen contributions of the initial stages of the process. (2) The population is enough large so that the sample fluctuations due to the finite population size can be neglected; the only source of fluctuations is the random nature of the evolutionary landscape. The evolution of the population can be expressed by the selection equations of the Fischer–Eigen type [20, 21] generalized by Ebeling et al. [22]

$$\partial_t \rho(\mathbf{x}; t) = \rho(\mathbf{x}; t) [r(\mathbf{x}) - \langle r(\mathbf{x}; t) \rangle] + D \nabla^2 \rho(\mathbf{x}; t), \quad (\text{C.1})$$

where

$$\rho(\mathbf{x}; t) d\mathbf{x} \quad (\text{C.2})$$

is the density of individuals with a state vector between \mathbf{x} and $\mathbf{x} + d\mathbf{x}$, the diffusion coefficient D describes the possible mutation processes, the function $r(\mathbf{x})$ is the fitness variable given by Eq.(8) and

$$\langle r(\mathbf{x}; t) \rangle = \frac{\int r(\mathbf{x}) \rho(\mathbf{x}; t) d\mathbf{x}}{\int \rho(\mathbf{x}; t) d\mathbf{x}} \quad (\text{C.3})$$

is a weighted average of the fitness variable. It is easy to check that Eq.(C.1) with the definition (C.3) for $\langle r(\mathbf{x}; t) \rangle$ conserves the total number of individuals

$$\mathcal{N} = \int \rho(\mathbf{x}; t) d\mathbf{x} = \text{constant}. \quad (\text{C.4})$$

Apparently the evolution equation (C.1) for the population density is typical for a selectionist theory; however, within the framework of our approach, since the selection pressure is due only to the fluctuations of the landscape, which are purely random, Eq.(C.1) can be also considered as a neutralist evolution equation.

Following Ebeling et al. [22] the solving of the nonlinear evolution equation (C.1) can be reduced to a linear eigenfunction–eigenvalue problem of the Schrödinger type

$$D \nabla^2 \psi_\ell + [E_\ell - V(\mathbf{x})] \psi_\ell = 0, \quad (\text{C.5})$$

where the potential $V(\mathbf{x})$ is given by

$$V(\mathbf{x}) = -r(\mathbf{x}), \quad (\text{C.6})$$

and E_ℓ and $\psi_\ell(\mathbf{x})$ are the eigenvalues and the eigenfunctions of the Schrödinger equation (C.5). The complete solution of Eq.(C.1) is [22]:

$$\rho(\mathbf{x}; t) = \frac{\sum_u c_u \exp(-E_u t) \psi_u(\mathbf{x})}{\sum_u c_u \exp(-E_u t)} \mathcal{N}, \quad (\text{C.7})$$

where, at least in principle, the constants c_u can be evaluated from the initial condition for the population density. Note that, as the eigenvalues E_u and the eigenfunctions $\psi_u(\mathbf{x})$ are functionals of the random landscape $\phi(\mathbf{x})$, the solution (C.7) for $\rho(\mathbf{x}; t)$ is also a functional of the landscape $\phi(\mathbf{x})$:

$$\rho(\mathbf{x}) = \rho[\mathbf{x}; t | \phi(\mathbf{x})]. \quad (\text{C.8})$$

The stochastic properties of the population density $\rho(\mathbf{x}; t)$ can be expressed in terms of a characteristic functional

$$\mathcal{G}[Y(\mathbf{x}; t)] = \left\langle \exp \left(i \iint \rho[\mathbf{x}', t' | \phi(\mathbf{x})] Y(\mathbf{x}'; t') d\mathbf{x} dt' \right) \right\rangle, \quad (\text{C.9})$$

where the average is taken over the space of functions $\phi(\mathbf{x})$. The evaluation of the characteristic functional $\mathcal{G}[Y(\mathbf{x}; t)]$ is a very tough problem. Although the deriving of a closed form for $\mathcal{G}[Y(\mathbf{x}; t)]$ seems to be impossible, if the dependence (C.8) is known a perturbation expansion may be derived by expanding the functional $\rho[\mathbf{x}; t | \phi(\mathbf{x})]$ in a functional Taylor series. By means of this approach the characteristic functional for the population density $\mathcal{G}[Y(\mathbf{x}; t)]$ can be expressed in terms of the characteristic functional $Z[K(\mathbf{x})]$ of the landscape.

The above method for describing the evolution of the population density holds only in the late stages of the evolutionary process. The description of the evolution of the population in the early stages of development is even more complicated. Since in this period of time the process of landscape formation is still going on, the fitness variables $\phi(\mathbf{x}; t)$ and $r(\mathbf{x}; t) = v\phi(\mathbf{x}; t)$, depend not only on the state vector \mathbf{x} but also on time, the system is with dynamical disorder and the characteristic functional of the landscape becomes

$$Z[K(\mathbf{x}; t)] = \left\langle \exp \left(i \iint \phi(\mathbf{x}; t) K(\mathbf{x}; t) d\mathbf{x} dt \right) \right\rangle. \quad (\text{C.10})$$

For the evaluation of the dynamic characteristic functional $Z[K(\mathbf{x}; t)]$ it is necessary to know the stochastic properties of the time interval between two successive generations.

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