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Landscape structure and the speed of adaptation

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ABSTRACT

The role of fragmentation in the adaptive process is addressed. We investigate how landscape structure affects the speed of adaptation in a spatially structured population model. As models of fragmented landscapes, here we simulate the percolation maps and the fractal landscapes. In the latter the degree of spatial autocorrelation can be suited. We verified that fragmentation can effectively affect the adaptive process. The examination of the fixation rates and speed of adaptation discloses the dichotomy exhibited by percolation maps and fractal landscapes. In the latter, there is a smooth change in the pace of the adaptation process, as the landscapes become more aggregated higher fixation rates and speed of adaptation are obtained. On the other hand, in random percolation the geometry of the percolating cluster matters. Thus, the scenario depends on whether the system is below or above the percolation threshold.

1. Introduction

The field of landscape genetics has emerged ten years ago and aims to improve our understanding about the interplay between landscape environmental features and evolutionary processes. Landscape genetics couples ideas and developed tools from the established fields of landscape ecology and population genetics [1].

Landscape structure largely influences the distribution of genetic variation, amount of genetic variation and gene flow [2]. The detection of sharp genetics changes or discontinuities on a geographic zone and the correlation of these changes with landscape environmental features are the target of landscape genetics. It is important to understand how the gene flow influences the genetic structure of a population, since it can provide useful information about the factors that enable and prevent local adaptation [1,3].

Adaptation proceeds through the occurrence and subsequent fixation of advantageous mutations [4–9]. The speed at which natural populations evolve is tightly constrained to the distribution of individual's fitness in the population [10], which by its turn is strongly dependent on the distribution of genetic variation, amount of genetic variation and gene flow. These factors can operate synergistically and produce an unpredictable outcome on the rate at which populations adapt.

Only recently we have observed a growing interest of the population genetics' community to address adaptive evolution in spatially structured population models [11–13]. By spatially structured population model we mean that the population is arranged over a two-dimensional square lattice. The study of the adaptive process in a spatially explicit context has recently been boosted by the growing interest of investigating biofilms, which is actually the prevailing microbial lifestyle, whereby microbes attach to surface and then develop complex structures [14]. The study of adaptive responses to pathogen-induced selective pressure in humans has also motivated the study of evolutionary dynamics within the same framework [15–17]. An interesting finding is the observation that structuring affects the speed at which population adapts to the environment, a feature that is demonstrated empirically [18,19], and also corroborated by structured population models [11,20]. In fact these studies show that adaptation proceeds more slowly in a spatially structured environment than in one whereby competition is global (non-structured populations), especially in the regime of high mutation rates. Though, the previous studies make the simplifying assumption that the substrate is non-fragmented (all cells in the lattice are considered to be suitable for occupation), a condition which is hardly met in natural biofilms. Indeed, in a recent survey it was shown that microbial communities in aquatic ecosystems display a fractal pattern [21]. As argued by the authors, the formation of biofilms is greatly affected by diverse factors which include nutrient levels, medium types, light, and so on. In the study the reported values of fractal dimensions of the surface formed by the packed communities of microbes lie in the range 1.3–1.5. As another instance, for example, Asally et al. have studied the dynamics between cellular and mechanical processes during the self-organization of *Bacillus subtilis*

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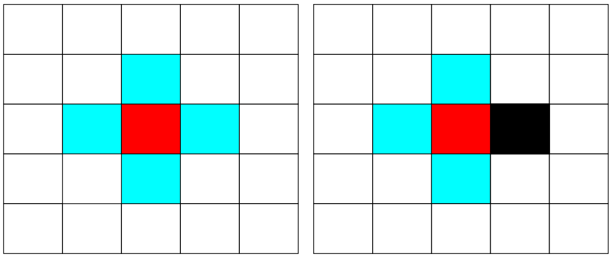

Fig. 1. Illustration of a non-fragmented (left panel) and fragmented (right panel) two-dimensional lattice as used in our simulations. The black cell in the right panel represents an unsuitable habitat. In the case of von Neumann neighborhood as assumed in our model the individuals placed in the five cells (left panel) or four cells for the fragmented case (blue + red) highlighted in the figure can reproduce and leave an offspring in the focal cell (red cell) for the next generation. The probability to reproduce in every reproduction event is proportional to the individual's fitness. This process is repeated for every cell in the lattice. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

cells into wrinkled biofilms (fractal structures) [22]. An interesting observed feature is that indeed the wrinkle structures constitute a population-level stress response of biofilms, a process which enhances the microbial resilience against environmental extremes.

To address the role of the landscape structure on the adaptive process within a theoretical framework we investigate a spatially structured population model in a fractal landscape whereby the degree of ruggedness can be tuned. The lattice is no longer homogeneous but rather fragmented such that some sites are considered to be unsuitable habitats. Two mathematical models are used to build up the fragmented landscapes: percolation maps and fractal landscapes. In the former, widely known as a simple example of a physical model that displays a phase-transition, the dilution is completely random such that every site is independently labeled as suitable (with probability p) or unsuitable (with probability $1-p$) [23]. Meanwhile, in fractal landscapes one can additionally tune the level of spatial autocorrelation, such that it is feasible to produce extremely rough or very compact surfaces by varying the Hurst parameter H.

The present study focuses on measuring how the topological properties of the landscape can affect the speed of adaptation in *in silico* populations. By changing the Husrt exponent H one modifies how compact the clusters are. This means that for low H different regions of the cluster will be connected by narrow corridors where supposedly beneficial mutations can spread. In short, the Hurst exponent tunes the gene flow. For high mutation rates the increase on the number of narrow corridors enhances the competition among segregating mutations, and hence can alter the strength of clonal interference, which affects the speed of adaptation. This investigation is carried out by means of extensive computer simulations. The remainder of the paper is organized as follows: The model is described in the next section. In Section 3 we describe the simulation results, and finally in Section 4 we present the concluding remarks.

2. Materials and methods

2.1. The model

We consider an asexual population of haploid organisms. The population is finite and the individuals are distributed over the suitable habitats of a two-dimensional regular lattice of linear size L. The fraction of suitable habitats is p, where $0 \le p \le 1$. Each suitable habitat is occupied by a single individual. The environment is always saturated, i.e., suitable habitats are not allowed to be empty. Periodic boundary conditions are assumed.

The population evolves following the Wright–Fisher model with non-overlapping generations, but rather than competing with every other individual for reproduction, they compete locally with their immediate neighbors (von Neumann neighborhood is considered). Because non-overlapping generations are assumed, at each time step all individuals on the population are replaced. The probability that an individual reproduces is proportional to its fitness. Each individual can contribute with offsprings at its position but also in its immediate neighborhood. Since von Neumann is considered each individual competes for reproduction in five cells. At each of these reproduction events the probability to be the parent of an offspring in a given cell is

$$p_j = \frac{\omega_j}{\sum_k \omega_k}, \qquad (1)$$

where p_j corresponds to the probability that individual j produces an offspring in a given cell and ω_j denotes its fitness value. The summation in Eq. (1) is taken over the five cells (immediate neighborhood and the focal cell), but only suitable habitats are viable to produce offspring (please see Fig. 1). The fitness ω_j is just given by $\omega_j = \prod_{\ell=1}^{n_b}(1+s_\ell)$, where n_b is the number of beneficial mutations present in the individual and s_ℓ is the selective effect of the ℓ-th mutation which by its turn is taken from an exponential distribution of mean $1/\alpha$. In the simulations α is set to 20, which corresponds to a mean-effect value of 5%. In the model we study adaptation under the assumption that deleterious mutations die quickly and survive at a negligible rate. This is justified on the basis of earlies studies about the dynamics of adaptation when the influx of beneficial mutation is high [24–26]. During reproduction, the offspring inherits the parent's genome but additional mutations occur at a constant rate U_b.

In the model migration is not explicitly assumed. Mutations can spread over the whole population by reproduction, since the most adapted individuals can reproduce and leave offspring in its neighborhood. In this way mutations spread in the form of waves [27].

2.2. Fragmented landscapes

2.2.1. Percolation maps

Percolation maps were the first neutral models considered in the field of landscape ecology [28,29]. The model was conceived to provide simple binary lattices of habitats and uses a single parameter p that controls the fraction of occupied cells. Each cell of the lattice is considered to be a suitable habitat with probability p and unsuitable with the complementary probability $q = 1 - p$. An amazing feature of the percolation model is the existence of a critical probability $p = p_c \approx 0.5927$ [30], dubbed percolation threshold, beyond this point a spanning cluster always arises in the thermodynamic limit. For values of p smaller than p_c the lattice is composed of many small and isolated clusters. The lower panels of Fig. 2 show instances of percolation maps for distinct values of the occupation parameter p. The middle panel highlights the percolating cluster which is red-colored.

2.2.2. Fractal landscapes

Despite the percolation maps have been applied to several studies it does not allow us to tune the level of spatial autocorrelation of the landscape. There are some methods to render landscapes with more complex spatial patterns. One of the most useful mathematical models for creation of correlated landscapes is the fractional Brownian motion (fBm) [31,32], a generalization of the central concept of Brownian motion. The most important characteristic of this mathematical model is that the correlation between successive steps is controlled by the parameter H, known as the Hurst exponent, which lies in the range $0 \le H \le 1$. When H is around one the landscape is smooth, and opposedly when H is