

Further Investigation of Random Fluctuation and Geometrical Effect of Disorder in Range Expansion of Competitive Species

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Abstract

This report is a follow-up study of [1], which explores the geometrical effect in range expansions. We further investigates the random fluctuations and asymmetric hotspot geometries on the survival dynamics of deleterious mutants using a simplified Eden model. We begin by reviewing the original work and providing a detailed explanation of the simulation scheme, which successfully reproduces the results of the original study. The statistical fluctuations are found to scale as expected, suggesting that there is no inherent bias in the simulation. This indicates that the non-trivial patterns observed, even in the absence of selective disadvantage, arise from statistical fluctuations. The impact of elliptical hotspots with different aspect ratios on mutant survival probabilities is studied. We find that vertically elongated hotspots enhance survival by reducing the critical separation between hotspots, while horizontally elongated hotspots decrease survival due to fewer total hotspots. These findings aligns with the result given in the original paper.

1 Introduction

The evolution of competitive species often results in spatial variations distinct from a well-mixed population. These variations arise from interactions with the environment, leading to a population state that differs significantly from the initial one (Fig. 1). In particular, the process by which invading species establish themselves in previously unoccupied areas, called range expansion [2], is important in many areas of biology, such as microbial colonies grown on Petrie dishes [3, 4], marine ecology [5] and human gene [6]. An extensive research to understand the dynamics of such phenomena has been made [1, 7–10] and additional references therein. For instance, [1, 7, 8] have employed the two-species (or multiple-species) Eden growth model [11], which uses stochastic approaches

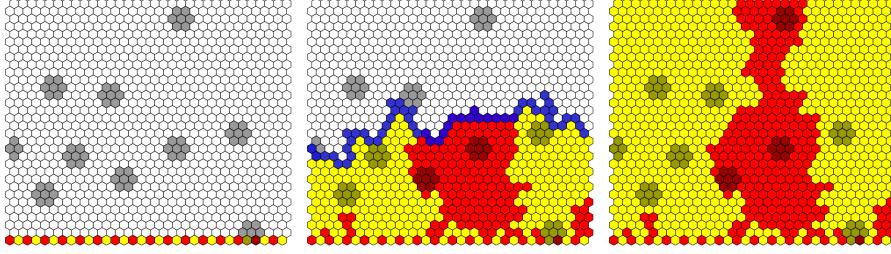


Figure 1: Range expansion of wild-type (red) and mutant (yellow) when $\mu = 0$ and $\nu = 6$. The leftmost figure illustrates the initial configuration of the two species and hotspots (gray). The blue line in the middle figure indicates the domain wall, and the rightmost figure shows the final state of the evolution, which is a mutant dominant state. The lattice size is 32×32 and $R = 2$ with $\phi = 0.2$.

to determine the evolution of species into unoccupied area based on a specific updating policies. Notably, [1] explored the effects of environmental disorder on range expansion, particularly the influence of geometry-induced factors. Here, disorder refers to random fluctuations in the environment that impact population growth. In this study, we primarily focuses on simulations of Eden model, leveraging approaches made in [1] to reproduce their result to understand the dynamics of range expansion with disordered environment and further explore the random fluctuations in the population pattern and effect of asymmetrical geometry of disorders.

This paper is organized as follows: Chapter 2 introduces the spatial growth model and summarizes the geometric effects of disorders given in [1]. It then discusses potential improvements and clarifies the main objectives of this study. Chapter 3 presents the simulation results, highlighting how random fluctuations in initial conditions shape mutant probability patterns. It also explores the impact of asymmetrical hotspot geometries, with a focus on ellipses. The report concludes with a summary of the key findings and their implications, along with suggestions for future research.

2 Model and Disorder

As briefly introduced in the previous chapter, we employ the simplified Eden model with two species, wild-type and mutant who has selective disadvantage $1 - s$ compared to the former, to simulate the range expansion in disordered environment. For our study, we set the mutation rate μ of wild-type into mutant to 0. The population evolves on a hexagonal grid, where the genetic identity of an empty site is determined by its occupied neighbors. The reproducing probability of each species on a certain site is therefore determined by the filling of its neighbors. Specifically, the mutant growth rate is defined as $\Gamma_m = (1 - s)\Gamma_w$,

with the wild-type growth rate normalized to 1, setting the overall scale. We assume that the genetic of a site remains unchanged once occupied. Environmental disorder is introduced by randomly placing circular patches, or hotspots, on the hexagonal grid with total hotspot area fraction ϕ . Within these hotspots, both species experience an amplified growth rate of $(1 + \nu)$, where ν represents the hotspot strength. We summarize the rules for our growth model as follows:

$$\begin{aligned}\Gamma_m &= (1 - s)\Gamma_w \quad \text{on plain site,} \\ \Gamma_i &= (1 + \nu)\Gamma_i \quad \text{on hotspot. } i = m, w.\end{aligned}\tag{1}$$

To implement the algorithms for simulation, let us define a bulk as a collection of sites whose all neighbors are occupied and a domain wall as a collection of occupied site that has at least one empty neighbor (so it can reproduce). We define a landscape as the initial configuration of wild-type, mutant, and hotspots, and a snapshot as the final state of a given landscape. The stochastic nature of the Eden model can generates different snapshots from the same landscape. The specific simulation scheme is as follows:

1. Initialize a landscape and a domain wall by visiting all occupied site.
2. Choose a random site from the domain wall according to Gillespie algorithm [12] whose implementation is outlined in [7]; each site in the domain wall is chosen to reproduce with probability proportional to the growth rate given in (1).
3. Among the empty sites of the chosen site, select one site with uniform probability and fill it with the same species.
4. Update the domain wall; we need to check (1) whether the chosen site still remains in the domain wall, (2) whether the newly occupied site is in the wall, and (3) whether the neighbors of the newly occupied site still remains in the wall.
5. Iterate until there is no site left in the domain wall.

The main part of the simulation is written in C++ and supports multi processing [13]. The example result of the simulation is shown in Fig. 1. Here, we used the initial condition given in [1], alternating wild-type and mutant. To characterize the randomness of our model, we introduce $M(x, y)$, the occupation probability of the mutant at certain site (x, y) within the same landscape. It is estimated by averaging the mutant counts at (x, y) over all snapshots of the same landscape. We also define the mutant frequency f_m , estimated by averaging the ratio of the number of mutant to the total lattice size over landscapes. The Fig. 2 and 3 shows the $M(x, y)$ and f_m respectively, averaged over 50 snapshots per landscape with 20 landscapes and region where the probability is larger than 0.5 is clipped to 0.5.

If the initial ratio of wild-type to mutant is 0.5 and there is no selection or environmental disorder, both wild-type and mutant will maintain equal frequencies of 0.5 and it is clear that $f_m \sim 0$ indicates the extinction of the mutant.

Thus, $f_m \sim 0.25$ serves as the midpoint and can be used as a threshold to determine mutant extinction. We see from Fig. 3 that above certain threshold in the phase space, mutant goes through extinction. According to [1], this behavior is non-trivial, as a naive mean-field approach predicts the extinction of the mutant for any (ν, s) when $s > 0$. They concluded that this phenomenon arises from the environmental disorder. In particular, they thoroughly investigated the effect of circular hotspots on the survival prospects of the mutant. By employing a geometric optics approach, they estimated the average separation between hotspots and derived an analytical formula in the (ν, s) parameter space that predicts the extinction threshold for the mutant. Here, we briefly sketch their key ideas. They first analyzed the effect of a single hotspot on mutant growth, deriving a threshold of mutant colony using geometric optics, which is the equation of an ellipse. Next, they calculated the length of the ellipse's axis aligned with the time axis (y direction in Fig. 1) and combined it with the average domain wall speed to determine the critical separation distance between hotspots. The central idea is that if hotspots are sufficiently dense, allowing the mutant colony to reach the next hotspot before the advancing domain wall of wild-type, the mutants can propagate and survive. Finally, they inverted the critical separation and used the average center-to-center distance of randomly distributed hotspots to derive an analytical formula predicting mutant extinction, given as

$$s(\nu, R, \phi) = \frac{2R^2}{k\lambda^2} \frac{\nu^2}{1 + \nu^2}, \quad (2)$$

where $k = 2\sqrt{2}/\sqrt{3}$ and the average center to center distance λ [14, 15] is

$$\lambda = \sqrt{2}R \sqrt{\frac{\pi}{-\ln(1 - \phi)}}.$$

The equation (2) can determined the contour $f_m \sim 0.25$ and we found that the reproduced result (Fig. 3) is consistent with (2).

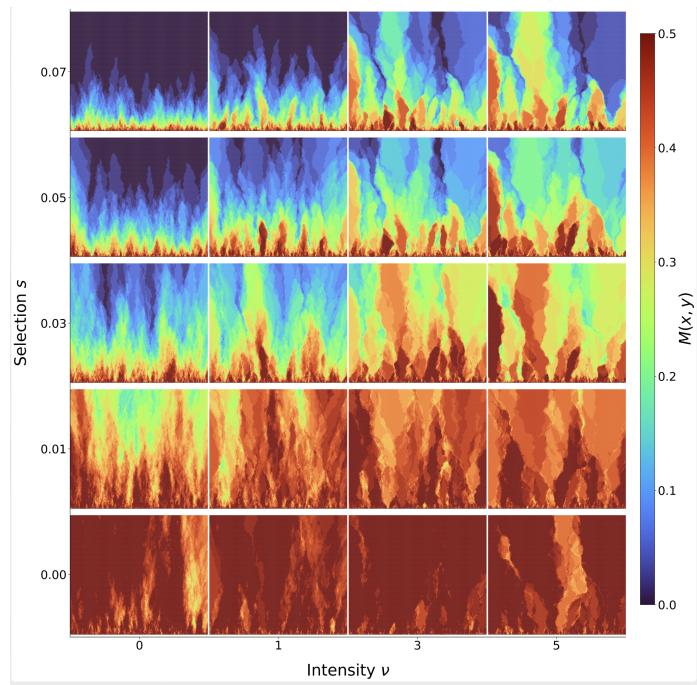


Figure 2: Mutant occupation probability $M(x,y)$ estimated by averaging 50 snapshots of the same landscape. The lattice size is 500×500 and $R = 5$ with $\phi = 0.25$.

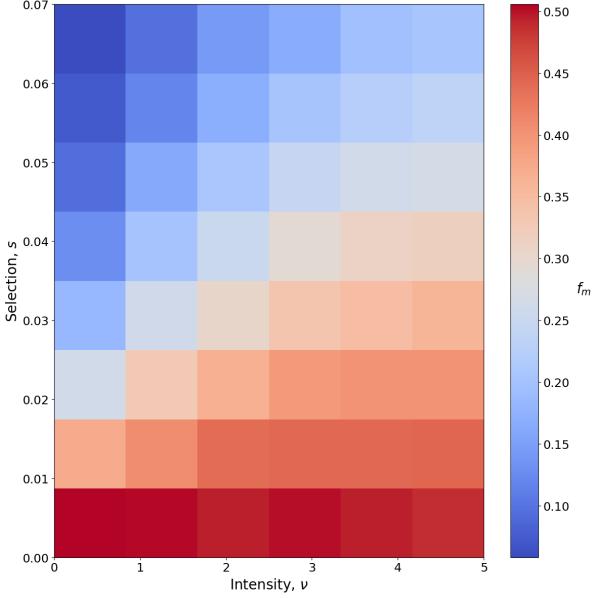


Figure 3: Mutant frequency f_m , generated by averaging 50 snapshots per landscape and 20 landscapes for each (ν, s) . The lattice size is 500×500 and $R = 5$ with $\phi = 0.25$.

We observe two interesting features in their results. First, patterns emerge in $M(x, y)$ even when $s = 0$, as shown in Fig. (2). This is unexpected, as one might assume no difference between averaged behavior of mutant and wild-type when $s = 0$. Additionally, one might wonder whether the survival probability of the mutant changes if the hotspot shape is asymmetric, such as an ellipse. Their analysis suggests that vertically elongated hotspots increase the mutant ratio by reducing the critical separation z . The goal of this report is to address these questions and explore extensions of the previous work. For the first part, we analyze the fluctuations of $\bar{M} = \sum_{x,y} M(x, y)/L_x L_y$ over different landscapes (recall that $M(x, y)$ is estimated at fixed landscape). Here, the fluctuation is defined in the usual way:

$$\sigma = \sqrt{\frac{\sum_{x,y} [M(x, y) - \bar{M}]^2}{L_x L_y}},$$

where the lattice size is $L_x \times L_y$, and the combined deviation over N different landscapes is given by

$$\bar{\sigma} = \frac{\sqrt{\sigma_1^2 + \sigma_2^2 + \dots + \sigma_N^2}}{N}.$$

For the second question, we repeat the analysis using elliptical hotspots with aspect ratios of $R_a/R_b = 3$ and $R_a/R_b = 1/3$, where R_a and R_b are the radii

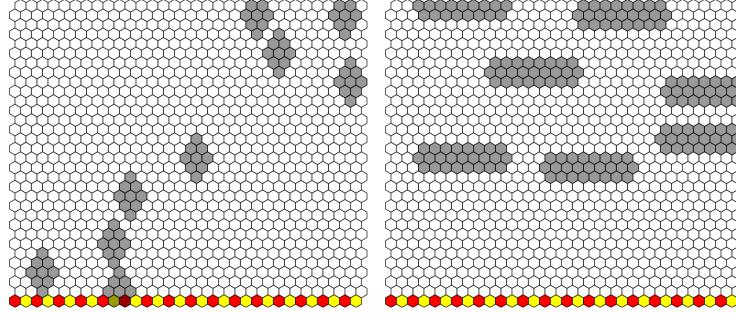


Figure 4: Left: Ellipse with $R_a = 2$ and $R_b = 6$. Right: Ellipse with $R_a = 6$ and $R_b = 2$.

of the horizontal and vertical axes of the elliptical hotspots, respectively. The following figures shows examples of ellipses in hexagonal lattice.

3 Results and Discussion

3.1 Random Fluctuation

We generated 500 snapshots per landscape and averaged the results over 50 different landscapes with each landscapes placing initial mutant at random points and the number of wild-type and mutant are the same at initial. The simulation results are shown in Fig. 5. Our analysis indicates no bias in the simulations, and the statistical fluctuations of $M(x, y)$ closely follow the expected behavior of $1/\sqrt{N}$.

3.2 Effect of Elliptical Hotspot

We generated 30 snapshots per landscape and averaged results across 20 different landscapes to determine the mutant frequency f_m . Each landscape employed an alternating initial condition of wild-type and mutant populations. The lattice size for all simulations was set to 500×500 , with an area fraction of $\phi = 0.25$. Figure 6 shows the mutant frequency when $R_a = 5$ and $R_b = 15$. It is evident that the survival probability of the mutant increases compared to the standard case where $R = 5$ shown in Fig. 3. This aligns with the results of the original study, as a vertically wider ellipse reduces the critical separation between hotspots. Figure 7 also illustrates f_m when $R_a = 15$ and $R_b = 5$. In contrast, we observe a decreased survival probability for the mutant. This is because increasing the horizontal extent of the hotspot, while keeping the area fraction fixed, reduces the total number of hotspots. Consequently, the likelihood of the initial mutant population contacting a hotspot decreases.

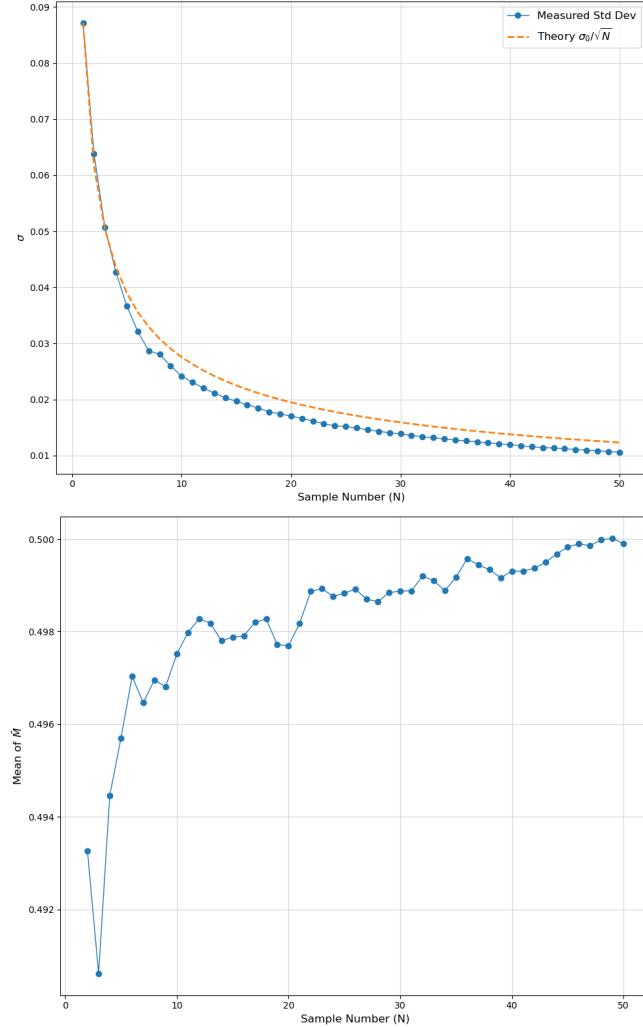


Figure 5: Upper: Standard deviations of \bar{M} over 50 different landscapes. Lower: Mean of \bar{M} over samples, defined as $\sum \bar{M}/N$. The sample number N denotes the number of landscapes

4 Conclusion

In this study, we reviewed and extended previous work on the role of environmental disorder in range expansions of deleterious mutants. Using the Eden model, we reproduced main results from prior research, confirming our simulation scheme is valid. We then examined the statistical fluctuations of spatial probability and found no bias in the simulation, indicating that the non-trivial

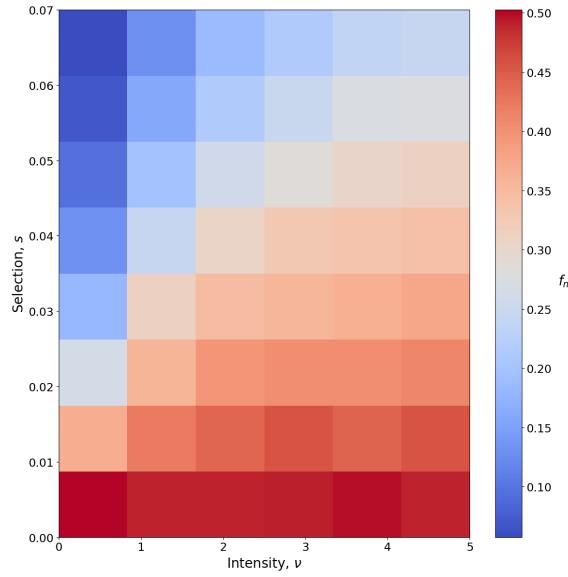


Figure 6: Mutant frequency when $R_a = 5$ and $R_b = 15$. Survival probability of mutant is increase compared to the normal case $R_a = R_b = 5$.

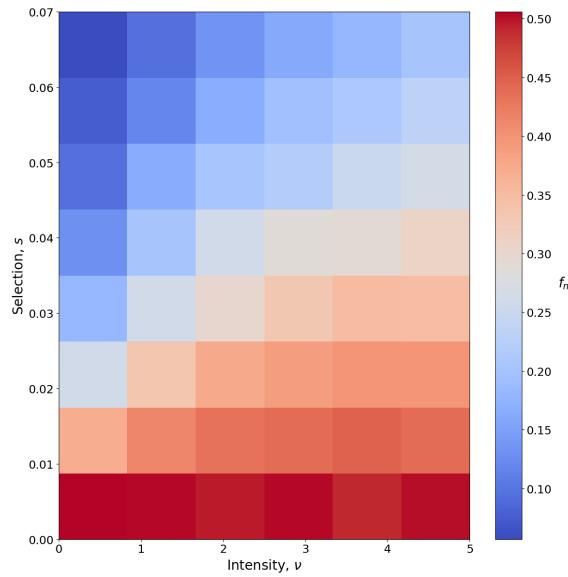


Figure 7: Mutant frequency when $R_a = 5$ and $R_b = 15$. Survival probability of mutant is increase compared to the normal case $R_a = R_b = 5$.

patterns observed, even in the absence of selective disadvantage, are a result of statistical fluctuations. We also explored the effects of elliptical hotspots with varying aspect ratios. Vertically wider hotspots were found to enhance mutant survival by reducing the critical separation required for propagation. Conversely, horizontally elongated hotspots lowered survival probabilities, as their reduced number limited the mutants' ability to reach subsequent hotspots. Possible future work could involve deriving an elliptical version of (2) and developing more accurate estimates of statistical fluctuations to better characterize and understanding of the patterns observed in Fig. 2.

References

1. Nuñez, J. G. & Beller, D. A. *Geometry-Induced Competitive Release in a Meta-Population Model of Range Expansions in Disordered Environments* 2024. arXiv: 2409.15221 [q-bio.PE]. <https://arxiv.org/abs/2409.15221>.
2. Korolev, K. S., Avlund, M., Hallatschek, O. & Nelson, D. R. Genetic demixing and evolution in linear stepping stone models. *Reviews of Modern Physics* **82**, 1691–1718. ISSN: 1539-0756. <http://dx.doi.org/10.1103/RevModPhys.82.1691> (May 2010).
3. Korolev, K., Xavier, J., Nelson, D. & Foster, K. Korolev KS, Xavier JB, Nelson DR, Foster KR.. A quantitative test of population genetics using spatiogenetic patterns in bacterial colonies. *Am Nat* 178: 538-552. *The American naturalist* **178**, 538–52 (Oct. 2011).
4. Korolev, K. S. *et al.* Selective sweeps in growing microbial colonies. *Physical Biology* **9**, 026008. <https://dx.doi.org/10.1088/1478-3975/9/2/026008> (Apr. 2012).
5. Ling, S. Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: A new and impoverished reef state. *Oecologia* **156**, 883–94 (Aug. 2008).
6. Sousa, V., Peischl, S. & Excoffier, L. Impact of range expansions on current human genomic diversity. *Current Opinion in Genetics Development* **29**. Genetics of human evolution, 22–30. ISSN: 0959-437X. <https://www.sciencedirect.com/science/article/pii/S0959437X1400080X> (2014).
7. Kuhr, J.-T., Leisner, M. & Frey, E. Range expansion with mutation and selection: dynamical phase transition in a two-species Eden model. *New Journal of Physics* **13**, 113013. ISSN: 1367-2630. <http://dx.doi.org/10.1088/1367-2630/13/11/113013> (Nov. 2011).
8. Lavrentovich, M. O. Critical fitness collapse in three-dimensional spatial population genetics. *Journal of Statistical Mechanics: Theory and Experiment* **2015**, P05027. ISSN: 1742-5468. <http://dx.doi.org/10.1088/1742-5468/2015/05/P05027> (May 2015).

9. Hallatschek, O. & Nelson, D. R. *Life at the front of an expanding population* 2008. arXiv: 0810 . 0053 [q-bio.PE]. <https://arxiv.org/abs/0810.0053>.
10. Paulose, J. & Hallatschek, O. The impact of long-range dispersal on gene surfing. *Proceedings of the National Academy of Sciences of the United States of America* **117** (Mar. 2020).
11. Eden, M. A Two-dimensional Growth Process. <https://api.semanticscholar.org/CorpusID:56348806> (1961).
12. Gillespie, D. T. A general method for numerically simulating the stochastic time evolution of coupled chemical reactions. *Journal of Computational Physics* **22**, 403–434. ISSN: 0021-9991. <https://www.sciencedirect.com/science/article/pii/0021999176900413> (1976).
13. Hwang, I. *Eden Growth Model Github* 2024. https://github.com/insungg/eden_growth_model (2024).
14. Xia, W. & Thorpe, M. Percolation properties of random ellipses. *Physical Review A* **38**, 2650 (1988).
15. Torquato, S. & Haslach, H. *Random Heterogeneous Materials: Microstructure and Macroscopic Properties* in (2005). <https://api.semanticscholar.org/CorpusID:121193023>.