Modelling the Role of Mutations and Density Independent Dispersal in Evolutionary Rescue

Melkior Ornik*

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Abstract

Faced with a strong and sudden deterioration of environment, a population encounters two possible options — adapt or perish. In general, it is not known which of those outcomes the environmental changes will lead to. Building on experimental research, we introduce a discrete-space, discrete-time model for environmental rescue based on the influence of population dispersal, as well as, potentially beneficial, mutations. Numerical results obtained by the model are shown to correspond well to experimentally obtained data.

KEYWORDS: EVOLUTIONARY RESCUE, DENSITY INDEPENDENT DISPERSAL, MUTATIONS, MATHEMATICAL MODEL

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1 Introduction

The ability of a species to persevere in quickly deteriorating environments has been historically noted, with particular emphasis placed on the notorious case of peppered moths [3, 4, 8, 9]. Multiple examples of rapid evolution caused by various stressors have been listed in [11]. More particularly, Bell and Gonzalez published a series of experimental findings of evolutionary rescue in yeast [1, 2, 7]. Several factors possibly contributing to the phenomenon have been proposed: behavioural responses [10], beneficial mutations [1] and stress history [7]. Involuntary movement of units — dispersal, was also examined in [2].

Experiments with metapopulations of yeast concentrated on measuring the rate of yield as a function of environmental stress, speed of environmental change and rates of dispersal. Fixing the speed of environmental change and rate of dispersal, a U-shaped pattern was found, indicating that populations undergoing more severe environmental impact may adapt more quickly than those in which the stress is existent, but less severe. Such a behaviour was hypothesised to result from an increase in the fraction of beneficial mutations in populations undergoing increasing stress levels [2].

*Department of Electrical and Computer Engineering, University of Toronto, Toronto, ON, M5S 3G4, melkior.ornik@scg.utoronto.ca

2 Discrete Mathematical Model

Based on the findings and hypotheses in [2], the proposed model considers two possible contributing factors: dispersal and mutation. The model considers n genotypes living on a finite number of patches. In each step, the populations first disperse (involuntarily and according to some function of time), after which each unit reproduces, its rate reproduction function of the current amount of stressor on the patch it currently resides on. To each of the genotypes corresponds its *optimal stress level* – a real number in $[0,1]$ at which the growth rate of the population of a certain genotype is highest.

Thus, the objects at play are:

- n different genotypes, labelled with 1, 2, ..., n, and with optimal stress level of $a_1, a_2, \ldots, a_n$, respectively,
- finite set Ω – discretization of the species living space,
- discrete time $t \in \mathbb{N}_0$.

The populations will further be denoted by function $P : \mathbb{N}_0 \times \Omega \times \{1,2,\ldots,n\} \to \mathbb{R}_0^+$, where $P(t,x,i)$ represents the number of units of genotype i at patch x, at time t.

2.1 Dispersal

Population scattering is given by function $w : \mathbb{N}_0 \times \Omega \times \Omega \to [0,1]$, where $w(t,x,y)$ represents the proportion of organisms residing at x at time t that move to y at that time. Clearly, an additional requirement of

$$\sum_{y \in \Omega} w(t,x,y) = 1$$

for all $t \in \mathbb{N}_0$ is given, as well as a natural expectation of

$$w(t,x,x) \ll w(t,x,y)$$

for all $y \neq x$. The latter serves only as an intuitive guideline: in a (short) time step, we expect most units to stay at the same place. However, it is mathematically completely irrelevant and plays no part in the model itself.

Considering the above description of the involuntary scattering model, the dispersal component of the step is naturally given by

$$\tilde{P}(t,x,i) = \sum_{y \in \Omega} w(t,y,x) P(t,y,i), \tag{1}$$

where $P(t,y,i)$, again, signifies the population of i-th species at location y, at the beginning of time step t, and $\tilde{P}(t,x,i)$ represents the population of i-th species at location x after dispersal in time step t.

Example 1. *A trivial example of a scattering function is given by $w(t,x,y) = \delta_{xy}$ for all $t \in \mathbb{N}_0$, $x,y \in \Omega$, where δ_{xy} is the Kronecker delta, equalling 1 if $x = y$ and 0 otherwise. In that case, there is no real scattering, as all the units just stay in place. Hence,*

$$\tilde{P}(t,x,i) = P(t,x,i)$$

for all $t \in \mathbb{N}_0$, $x \in \Omega$ and $i \in \{1,2,\ldots,n\}$.

Example 2. *A slightly less simple uniform scattering function proves to be useful when we know there is dispersal, but might not know the actual dispersal pattern:*

$$w(t,x,y) = \begin{cases} 1-p & \text{if } x = y, \\ \frac{p}{\text{card}(\Omega)-1} & \text{if } x \neq y, \end{cases}$$

for all $t \in \mathbb{N}_0$, $x,y \in \Omega$, where p in $[0,1]$. This scattering function, for a small positive value of p, is used (as global dispersal) in the numerical results discussed in the following section.

In this case,

$$\tilde{P}(t,x,i) = (1-p)P(t,x,i) + \frac{p}{\text{card}(\Omega)-1} \sum_{y \in \Omega} P(t,y,i).$$

We note that the scattering function given in the previous example is a special case of this one, for $p = 0$.

2.2 Reproduction

Having finished with dispersal, we turn our attention to the second component of the model: reproduction. Mutations, as the other factor we are investigating that contributes to evolutionary rescue, occur during this stage.

In the model, the rate of reproduction entirely depends on the stress level of the environment. The process is asexual and we assume there are sufficient nutrients to support any number of organisms on any single patch. Thus, at optimal stress level, reproduction follows the basic exponential population model: at every step, every genotype produces $1+\varepsilon$ its current population of new units, for a small positive ε.

We assume that all the organisms, having reproduced, immediately die. This simplification is merely technical and can be easily compensated for by adjusting the reproduction (and mutation) rates, as a unit producing n offspring and immediately dying is the same as a unit producing $n-1$ offspring and continuing to live.

The stress level is given by $f : \mathbb{N}_0 \times \Omega \to [0,1]$, and we assume that no genotype can survive at stress levels outside the interval $[0,1]$. Again, as an intuitive guideline, we note that the "natural" stress level of the patches should be close to 0 and we expect the most common genotype to be the one with optimal stress at 0 or close to it, although there is no mathematical reason in the model requiring it to be so.

As mentioned, when the stress level is optimal for it at a given location, every genotype produces $1+\varepsilon$ times its current population of new units. When the stress level is not optimal, genotype i at time t and location x produces $1+\varepsilon-(a_i-f(t,x))^2$ offspring. Thus, the reproductive yield is reduced by the square of difference between the current and the optimal stress level for a certain genotype. We note that $0 \leq (a_i - f(t,x))^2 \leq 1$, and thus, at each step, between ε and $1+\varepsilon$ new units will be produced.

2.3 Mutations

Of the offspring produced, we expect most to be of the same genotype, while a minority will be mutants of other genotypes. Analogously to the dispersal pattern, this is modelled by function $m : \{1,2,\ldots,n\} \times \{1,2,\ldots,n\} \to [0,1]$, where $m(i,j)$ indicates the proportion of offspring of species i that are of species j. Again, we require

$$\sum_{j=1}^{n} m(i,j) = 1$$

and expect

$$m(i,j) \ll m(i,i)$$

for all $i \neq j$, $i,j \in \{1,2,\ldots,n\}$.

Example 3. *As with dispersal patterns, $m(i,j) = \delta_{ij}$ for all i,j ensures there are no mutations, and*

$$m(i,j) = \begin{cases} 1-\rho & \text{if } i = j, \\ \frac{\rho}{n-1} & \text{if } i \neq j, \end{cases}$$

for $\rho \in [0,1]$, ensures uniform mutation rates.

Clearly, the situation with mutation is not necessarily as straightforward as with dispersal patterns. More precisely, while taking uniform dispersal rates may not be seen as a critical simplification, it is hard to believe the probability for mutation between two genotypes with reasonably close optimal stress levels will be the same as the one for genotypes whose optimal stress levels are much further away.

Motivated by the above thinking and without any knowledge of the nature of organisms involved, one could develop a simple random walk model, where the probability of mutating from genotype i to genotype j is proportional to the distance in their optimal stress levels. However, this limits the mutations to only "jumping" to the "previous" and "next" genotype in one step.

Example 4. *Let us assume without loss of generality that $a_1 < a_2 < \ldots < a_n$. Then*

$$m(i,j) = \begin{cases} 1-\rho & \text{if } i = j, \\ \rho \cdot \frac{a_{i+1}-a_i}{a_{i+1}-a_{i-1}} & \text{if } j = i-1, \\ \rho \cdot \frac{a_i-a_{i-1}}{a_{i+1}-a_{i-1}} & \text{if } j = i+1, \\ 0 & \text{if } |i-j| > 1, \end{cases}$$

again for $0 \leq \rho \leq 1$ and $1 < i < n$. If $i = 1$ or $i = n$, we have

$$m(1,j) = \begin{cases} 1-\rho \cdot \frac{a_3-a_2}{a_3-a_1} & \text{if } j = 1, \\ \rho \cdot \frac{a_3-a_2}{a_3-a_1} & \text{if } j = 2, \\ 0 & \text{if } j > 2 \end{cases}$$

and, analogously,

$$m(n,j) = \begin{cases} 1-\rho\cdot\frac{a_{n-1}-a_{n-2}}{a_n-a_{n-2}} & \text{if } j=n, \\ \rho\cdot\frac{a_{n-1}-a_{n-2}}{a_n-a_{n-2}} & \text{if } j=n-1, \\ 0 & \text{if } j<n-1. \end{cases}$$

In other words, genotypes with extreme optimal stress levels mutate at the same rate at which they receive mutations.[1]

The mutation model in Example 4, while not being trivial to the extent of Example 3, is again admittedly a simplification. However, given the lack of information on the genetic basis for stress in such an abstract model, it seems an appropriate one to use in later numerical results.

Multiple other models for genetic drift have been proposed: the classical one is the Wright–Fisher model [6, 12], and its modifications and alternatives have been discussed at length in [5]. However, these often require further information about the genotypes to be useful. In short, unlike the relatively safe (and symmetric) bet for dispersal, one can not, without any further information, easily decide on a neutral model for mutations.

After digressing into discussion of genetic drift, we go back to our basic reproduction model. Taking into account all of the above, we finally obtain the following equation for the reproduction stage:

$$P(t+1,x,i) = \sum_{j=1}^{n} m(j,i)\left(1+\varepsilon-(a_j-f(t,x))^2\right)\tilde{P}(t,x,j). \tag{2}$$

Plugging the equation (1) for dispersal into (2), we obtain

$$P(t+1,x,i) = \sum_{j=1}^{n}\left(m(j,i)\left(1+\varepsilon-(a_j-f(t,x))^2\right)\sum_{y\in\Omega} w(t,y,x)P(t,y,j)\right). \tag{3}$$

3 Numerical Results

The foundation for the numerical simulations of the model was the experiment on well plates discussed in [2]. In our case, the physical space in the simulations consisted of 101 patches considered to be on a straight line.[2] 11 genotypes were used, with uniformly distributed optimal stress levels ($a_i = \frac{i-1}{10}$ for $i \in \{1,2,\ldots,11\}$). At time $t = 0$, stress was set to 0 at all points, and 98% of the population was of genotype 1, i.e. the one with optimal stress 0. The other 2% were uniformly distributed among other genotypes, each accounting for 0.2% of the population.

The mutation function used was the one discussed in Example 4, with $\rho = 0.03$. Finally, ε was set to 0.04.

[1] In this example, we obviously assume $n \geq 3$.

[2] The latter is useful merely as providing intuition and natural reasoning to various dispersal patterns.

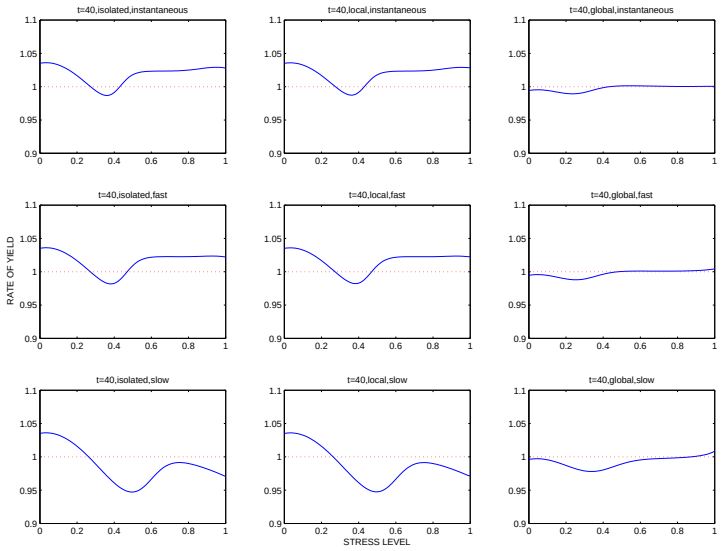

Figure 1: Rates of yield at patches with certain stress level, at time $t = 40$. Rate of yield of 1 denotes a patch with constant population.

Analogously to the yeast-and-salt experiment in [2], the following modes of dispersal and stress were used: dispersal could be *isolated* (nothing ever changes locations), *local* (units move to one of the neighbouring patches with probability $p = 0.05$, except at the endpoints, where the probability is $p/2 = 0.025$) or *global*, where units move uniformly to any other patch with total probability $p = 0.05$.

The final stress level was the same in all simulations — at $t = 40$, the stress level at one end of the line of patches was 0, while at the other end, it was 1. The patches in-between had stress levels proportional to their position. However, those stress levels were reached in three different ways: *instantaneous* (at all times $t \geq 1$, $f(t,x) = \frac{x-1}{100}$, where patches were denoted by 1, 2, ..., 101), *fast* ($f(t,x) = \frac{t}{5} \cdot \frac{x-1}{100}$ for $t \leq 5$, and $f(t,x) = \frac{x-1}{100}$ after $t = 5$) and *slow* ($f(t,x) = \frac{t}{20} \cdot \frac{x-1}{100}$ for $t \leq 20$, and $f(t,x) = \frac{x-1}{100}$ after $t = 20$).

Running the simulation for the above nine combinations of stress and dispersal, the model results in the population dynamics (at $t = 40$) given in Fig. 1.

The results show marked qualitative similarity to the outcomes of the experiment in [2]. In particular, a U-shaped relationship discussed in the above paper is noticeable. Furthermore, the results confirm the intuitive conjecture that population mixing through dispersal helps the areas containing genotypes which are having problems adjusting, while it hurts the areas not undergoing stress and well-adjusted areas.

Finally, as the responses to differences in speed of environmental deterioration show, fast deterioration indeed contributes to quicker adaptation, especially in the cases

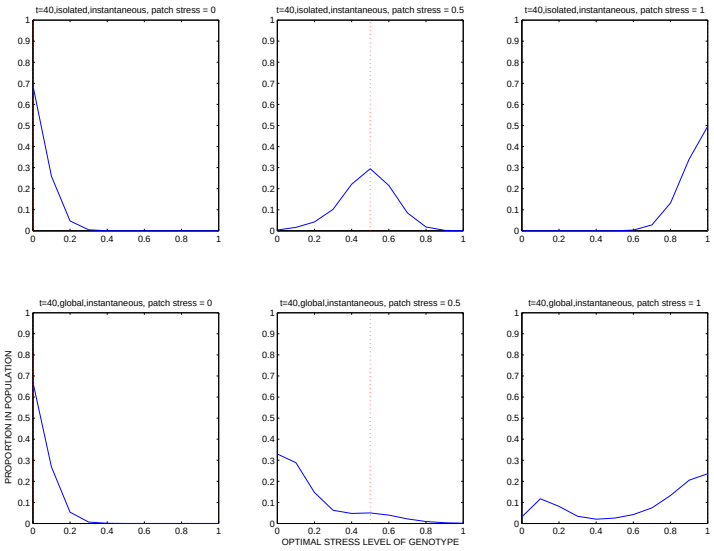

Figure 2: Populations of certain genotypes at patches with certain stress level, at time $t = 40$.

of high stress levels.

The model also allows for explicitly determining the most prevalent genotype on each patch, and determining the proportion of each genotype in the population on the patch. This is given in Fig. 2, where the results show significant differences between behaviours with global dispersal turned on and without it. In fact, while the genotype closest to the current level of stress on the patch is the most represented one in the case where there is no dispersal, this occurs much less notably when dispersal is turned on.

Finally, it should be noted that the results depend heavily on our choice of parameters such as ρ, p and ε. Nonetheless, the results obtained for other (reasonable) parameters are qualitatively similar to those given in Figures 1 and 2.

4 Conclusions

The model constructed in Section 2 supports the findings of [2] that beneficial mutations and dispersal patterns can play a large role in environmental rescue. In particular, results given in Section 3 show that dispersal indeed plays a key role in moderating the growth rates of metapopulations exposed to prolonged periods of stress. Furthermore, simulations based on this model support the results claiming adaptation is faster and more effective in the cases of more substantial and faster environmental deterioration.

As noted above, the most difficult hurdle to improving the realism of the above model is finding the appropriate genetic drift function. The downside of the level of

abstractness provided is the lack of any real genetic information on which to base the mutation function. As the results have shown, the function used in Example 4 works reasonably well and corresponds well to the particular experimental data obtained for yeast, but can certainly be improved by using real information for a particular species.

Further generalizations of the model could incorporate the notions of continuous time and space. However, implementing continuous space would likely result in a much more difficult model involving Lebesgue integration. It is not reasonable to expect that such a model would be analytically solvable and, hence, its practical uses would be limited to numerical simulations, which would again discretize the state space.

In general, apart from confirming the previously experimental results, the model opens possibilities for examining genotype prevalence, as done in the previous section, and for further experimentation with the levels of stress history [7].

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