

# Metapopulation Dynamics: Global Environmental Stochasticity

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# Abstract

The study of environmental effects in metapopulations provides essential information for conservation ecology. Fragmented or patchy populations are more robust to surviving stochastic fluctuations that could otherwise cause extinction of the population. Migration between patches can save a patch from extinction and also allows for recolonization of unoccupied patches. Individual-based, stochastic metapopulation models provide a theoretical framework for studying a wide range of populations. The stochasticity included in these models introduces interesting questions regarding the extinction risk of a population, both empirically and theoretically. We ask the question: how does environmental stochasticity on a global spatial scale affect a metapopulation? A stochastic, discrete-generation Ricker model is used to study the environmental fluctuations affecting a metapopulation, using numerical simulations. This model is extensively tested for different types of stochasticity, especially local environmental stochasticity. Examining the simulations for global environmental stochasticity we find that patch population sizes become correlated in size, as they all experience the same environmental conditions. Comparing the strength of the rescue effect for local and global fluctuations we find the rate of local extinction to be almost similar. Further analysis shows that the rescue effect is still present, although overshadowed by stochasticity when the patch population size is low. Continuing on this study one could investigate different probability distributions for including global environmental stochasticity in the birth rate. Also of interest is the analytical analysis for a metapopulation subjected to global environmental stochasticity, if possible.



# Contents

<b>Abstract</b>	<b>3</b>
<b>1. INTRODUCTION</b>	<b>1</b>
1.1. Metapopulations . . . . .	1
1.2. Local Stochastic Dynamics . . . . .	3
1.2.1. Global versus to Local Stochasticity . . . . .	3
<b>2. The Model</b>	<b>5</b>
2.1. Metapopulation model . . . . .	5
2.1.1. Recruitment Phase . . . . .	6
2.1.2. Dispersal Phase . . . . .	7
2.2. Full Stochastic Simulation . . . . .	8
<b>3. Global Environmental Stochasticity</b>	<b>11</b>
3.1. Weak Environmental Stochasticity . . . . .	11
3.2. Strong Environmental Stochasticity . . . . .	12
3.3. Observing Patch Populations . . . . .	13
<b>4. The Rescue Effect</b>	<b>17</b>
4.1. Measuring the Strength of the Rescue Effect . . . . .	17
4.2. Measuring the Occupancy Rate . . . . .	18
<b>5. Conclusion</b>	<b>21</b>
<b>Bibliography</b>	<b>23</b>
<b>A. Alternative Continuous Time Model</b>	<b>25</b>
A.1. Continuous time Metapopulation Model . . . . .	25
<b>B. Numerical Simulations</b>	<b>27</b>
B.1. Pseudo Code for Discrete Time Stochastic Simulations . . . . .	27
B.2. Transition Probabilities . . . . .	29
<b>C. Patch Perturbations</b>	<b>31</b>
C.1. Perturbing a single patch . . . . .	31



# 1. INTRODUCTION

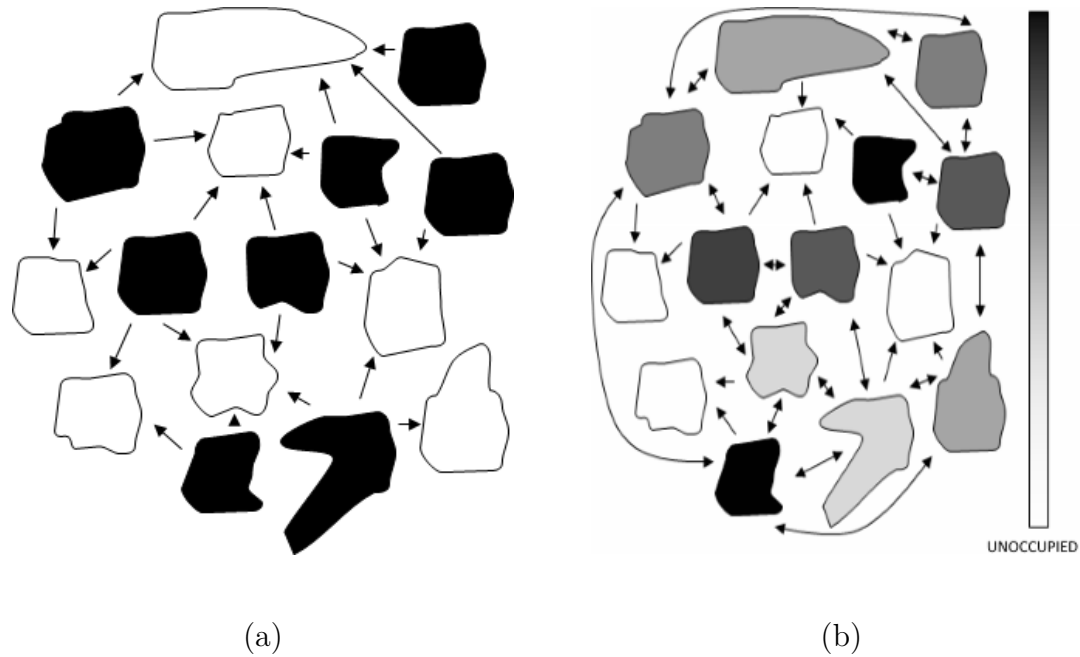
The study of metapopulation dynamics has undergone various transformations since its formalized introduction by Levins [1]. We discuss the essence of a metapopulation and how the study thereof has evolved to the current state of the art. Our study, specifically, incorporates the fluctuating environmental conditions affecting populations, hence referred to as stochasticity. The concept of global, as opposed to local, environmental stochasticity is discussed in this section together with the range of other stochastic effects that can be experienced by a population.

## 1.1. Metapopulations

The study of metapopulations provides valuable insight into the persistence of populations under stress from habitat destruction or fragmentation [2]. Organisms subjected to empirical and theoretical studies range from bacteria to animal species, proving the applicability of metapopulation models. Metapopulations are commonly represented as a set of spatially separated populations, interacting through immigration between populations. Each individual population is alternatively referred to as a patch. In the classical Levins model a patch is observed as either occupied or unoccupied. This model is well studied, both theoretically [3, 4, 5] and empirically [6, 7]. The equation has a constant patch colonization rate  $c$ , a constant patch extinction rate  $e$  and  $N$  number of occupied patches. During a time  $dt$  an unoccupied patch might become occupied with rate  $cNdt$ , or an occupied patch might become extinct with rate  $eNdt$ . Together the change in the number of occupied patches during time  $dt$  is

$$\frac{dN}{dt} = cN(1 - N) - eN \tag{1.1}$$

Since the first introduction of the Levins model, it has become increasingly clear that the local, within patch dynamics could not be discounted [8, 9]. The stochastic fluctuations of individual patch populations could lead to sporadic local extinction, which in turn could lead to the extinction of the whole metapopulation. The analysis of local dynamics incorporated the study of the so called 'rescue effect'. The rescue effect was introduced by Brown & Kodric-Brown [10] and further developed by Hastings [11, 12]. Immigration of individuals into a patch on the brink of extinction



**Figure 1.1.:** Illustrating the significant difference between the classical Levins model (a), where a patch is either occupied or unoccupied, and the individual stochastic models (b). Each spot represents a population and all the populations together collates to a metapopulation

can save that patch from extinction, providing a buffering effect termed the 'rescue effect'. This effect serves as a counteracting mechanism for the adverse periods of stochasticity experienced by local populations.

In order to model local patch dynamics, Lande *et al.* [13] introduced a diffusion approximation as a way to analytically analyze metapopulations. They described metapopulation dynamics as consecutive, isolated, extinction and recolonization events. This method had the limitation of relying on low immigration rates, but introduced a better understanding of local patch dynamics. The advantage of explicitly modelling the number of individuals in a patch through birth, death-processes and, subsequently, emigration and immigration on the metapopulation scale was demonstrated by, among others, Drechsler and Wissel [14] and Newman *et al.* [15]. Population dynamics can thusly be studied on the brink of extinction [16], allowing us to determine the most likely route to extinction and in due course implement counter-measures. Four central processes govern the dynamics of explicit models, namely: birth, death, emigration and immigration. The corresponding equations differ depending on implementation.

Although we will not address 'extinction risk' specifically, the definition is still of importance. Higgins [17] clarifies extinction risk as the probability of all patch populations becoming extinct. No recovery is possible from this state. When stochasticity



is introduced in metapopulation dynamics, a metapopulation with a finite number of patches may achieve a quasi-steady state, but a series of chance events must eventually lead to metapopulation extinction [16]. As we will see, for the case of infinite number of patches, the dynamics become deterministic again nullifying the probability of complete extinction.

## 1.2. Local Stochastic Dynamics

Stochasticity is critical in metapopulations models. Feller already demonstrated in 1939 [18], that where population models under the influence of stochastic fluctuations might go extinct, similar deterministic models predict indefinite survival. Stochasticity is modelled in the local dynamics, allowing for variance in the population growth. Demographic stochasticity and environmental stochasticity are the two most commonly defined sources of fluctuations [19]. The first simulates the random birth, death-event of an individual. This captures the difference in chance events, offspring production and death [20]. The second accounts for exogenous factors, such as rainfall and temperature fluctuations, causing patch-wide devastation. Environmental stochasticity poses a risk for even large population to go extinct. A further stochastic effect included in the models presented by Melbourne and Hastings [21] is demographic heterogeneity. Contrary to demographic stochasticity, which captures chance events, demographic heterogeneity accounts for the variation in birth and death rates between individuals [22]. In our model when we refer to demographic stochasticity, we refer to both the stochasticity of demography as well as demographic heterogeneity, following the convention of [23]. Together these three sources of variation are included in our models providing a complete assessment of the survival capabilities of a population.

### 1.2.1. Global versus to Local Stochasticity

A question we want to answer is, how would global environmental stochasticity affect the survival of a population, compared to current implementations of local environmental stochasticity [17, 21, 23]? Global environmental stochasticity can be interpreted as a sequence of environmental fluctuations, favorable or unfavorable, affecting all patch populations simultaneously and equally. Contrary to local environmental stochasticity, where each patch is affected individually and differently by environmental fluctuations. We regard the study of global environmental stochasticity to be of importance, especially for microscopic species, since we expect to see a much higher extinction rate in the case of global fluctuations. All populations have to endure unfavorable conditions together. A metapopulation currently enduring an unfavorable state would be unable to effectively recolonize patches which are extinct, as all populations are simultaneously under stress.



## 2. The Model

The discrete Ricker model provides the underlying structure for our metapopulation simulations. In this section we explore and expand the model to incorporate metapopulation dynamics subject to global environmental stochasticity. This includes defining the probabilistic transition structure for a metapopulation in the current generation to evolve into the next generation. The rescue effect measurement that will be used to comparatively study the global environmental stochasticity versus local environmental stochasticity is also discussed in this section.

### 2.1. Metapopulation model

Modelling an individual-based stochastic metapopulation can be achieved in several ways. Our model follows the formulation done by Eriksson *et al.* [16]. The local dynamics is derived from the deterministic Ricker population model [24],

$$E[N_{t+1}] = RN_t \exp(-\alpha N_t) \tag{2.1}$$

and includes stochasticity factors according to the expanded model in [21]. In (2.1)  $N_t$  is the population size in generation  $t$ ,  $R$  the density independent per-capita growth rate and  $\alpha$  incorporates the density dependent effects.

For a metapopulation study the effects of stochasticity are included by randomly modifying the growth rate  $R$ . This stochastic, discrete, metapopulation model was compared to a lab population of *Tribolium castaneum* by [21], and for the inclusion of demographic and environmental stochasticity an acceptable regression fit was found. This study also provides us with a range of realistic applicable parameters for which we can analyze our model. For comparison to the discrete dynamics, Appendix A.1 briefly presents the continuous time, individual-based, stochastic analytical model.

In our model the metapopulation consists of  $N$  population patches connected by dispersal. We focus on a large number of patches and hope this results in universal, simple, conclusions. The patch populations evolve in discrete, non-overlapping generations. Each generation consists of two phases. The first being recruitment, the production of progeny by adults, followed in the second phase by dispersal of progeny to other patches. All adults are removed after producing progeny, completely replaced by their offspring and thus the definition of discrete non-overlapping generations. We expect the metapopulation to achieve a quasi steady-state where

the metapopulation will persist until a sequence of stochastic events must drive it extinct.

A very effective method for evaluating the evolution of a metapopulation is to describe the current generation (denoted as  $t$ ) of patch population sizes in the form of a frequency vector  $f_i(t)$ , where  $i$  is the patch population size [23]. This vector can be evaluated at the different phases of a generation as well as between generations.

### 2.1.1. Recruitment Phase

During recruitment, adults have a Poisson distributed number of progeny with rate  $R_i$  for individual  $i$ . The Poisson-distributed parameter accounts for the natural fluctuations of the birth-death process. To include demographic and environmental stochasticity,  $R_i$  must itself be a random process. In order to determine  $R_i$  for each individual  $i$  during the reproduction phase of a generation, we start with modifying the rate,  $R$ . As in [17],  $R$  is defined to be the mean per-capita growth rate in absence of other stochastic factors.

When simulating a metapopulation, environmental stochasticity modifies the growth rate first, as its effects has the broadest scope. From  $R$  it determines a mean recruitment rate  $R_E$  based on environmental fluctuations.  $R_E$  is in our case gamma-distributed with mean  $R$  and shape parameter  $k_E$ .  $R_E$  is either applied to the whole metapopulation (global environmental stochasticity) or patch-wise (local environmental stochasticity). Thereafter, individual recruitment rates  $R_i$  are determined independently by a gamma-distributed variable with mean  $R_E$  and shape parameter  $k_D$ , accounting for demographic stochasticity. Higgins [17] argues gamma distributions are biologically realistic for modifying the Poisson recruitment rates [25, 26].

Finally, density dependent survival for offspring to adulthood is independent probabilistic  $\exp(-\alpha n)$ , where  $n$  is the number of adults in a population patch and  $\alpha$  regulates the strength of density dependence. Density dependent survival is similar to the carrying capacity in alternative metapopulation models [17]. Taking it all together we can analytically define the transition probability of  $j$  adults producing  $i$  offspring for local environmental stochasticity, the same as found in Melbourne and Hastings, Supplementary Table 1 [21]:

$$P_{ij} = \int_0^{\infty} \frac{k_E}{R\Gamma(k_E)} \left(\frac{k_E R_E}{R}\right)^{k_E-1} e^{-\frac{k_E R_E}{R}} \binom{i+k_D j-1}{k_D j-1} \times \left(\frac{R_E e^{-\alpha j}}{k_D + R_E e^{-\alpha j}}\right)^i \left(\frac{k_D}{k_D + R_E e^{-\alpha j}}\right)^{k_D j} dR_E \quad (2.2)$$

While the equation defines the transition probability for the local environmental model, the global environmental model requires the integration of Langevin equation, since the dynamics are no longer contained within patches and instead spans

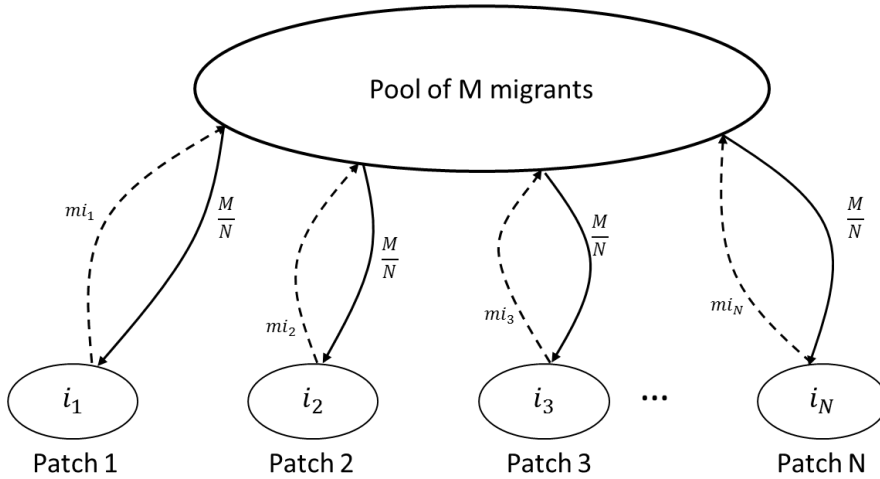
all patches in the metapopulation. We will rather use the full stochastic simulation to generate offspring in populations affected by global fluctuations.

At the end of the recruitment phase, we can describe the metapopulation in terms of an intermediate frequency vector  $f_i^R(t)$  after recruitment and density dependent survival. It describes the number of offspring produced:

$$f_i^R(t) = \sum_{j=0}^{\infty} P_{ij} f_j(t) \tag{2.3}$$

Now offspring are ready for the dispersal phase.

### 2.1.2. Dispersal Phase



**Figure 2.1.:** The dispersal process for individual-based, stochastic metapopulations. Each individual has probability  $m$  to leave patch  $n$  (patch of size  $i$ ),  $n = 1, \dots, N$ . The emigrant joins the pool of  $M$  migrants. From the pool of migrants an individual immigrates into a random patch, a patch thus has probability  $\frac{M}{N}$  of receiving any one immigrant. The whole migration process happens sequentially after progeny production and during the same generation. Similar to Figure 1 in [16]

The dispersal process is adapted from [5] by [16] for the case of individual-based, stochastic metapopulation models and is illustrated in Fig. 2.1. In our model we make three assumptions. First, there is no mortality during the dispersal phase. Secondly, there is no time separation during dispersal. An individual leaves a patch and arrives at the random destination patch in the same generation  $t$ . Lastly, as we focus on a large number of patches, we will have a common dispersal pool with

no spatial influence. The assumption of a spatially implicit model is tested in [23] concluding that the analytical model agrees well with the simulated results.

Each individual in a patch has probability  $m$  to disperse (emigrate) from a patch and join the pool of  $M$  migrants. The analytical fraction of emigrants  $f_i^D(t)$  is

$$f_i^D(t) = \sum_{j=1}^{\infty} \binom{j}{j-1} (1-m)^i m^{j-1} f_j^R(t). \quad (2.4)$$

A migrant can immigrate into any random patch. For a large number of patches the distribution of migrants arriving to each patch is Poisson-distributed. The expected number of individuals arriving to a patch is written as

$$I(t) = \sum_{i=0}^{\infty} m i f_i^R(t). \quad (2.5)$$

Taking Eqs. (2.2), (2.3), (2.4) and (2.5) together, we can write the frequency distribution for the next generation

$$f_i(t+1) = \sum_{j=0}^i \frac{I(t)^j}{j!} e^{-I(t)} f_{i-j}^D(t). \quad (2.6)$$

## 2.2. Full Stochastic Simulation

The structure in section 2.1 explains the proceedings of a metapopulation while Eqs. (2.2)-(2.6) define the analytical form. As found in [27] there is little variability in the (mean) population size for  $N$  very large. In the limit  $N \rightarrow \infty$ , the dynamics become deterministic and the equations can be successfully applied in this case. This allows us to compare our full stochastic simulations, for large values of  $N$  to the deterministic case, verifying our stochastic models. Full stochastic simulations involve random number generation from the probability distributions describing each of the stochastic processes. As indicated previously, to measure the effects of global environmental fluctuations we must analyze stochastic simulations, since the analytical equations are not accessible. Pseudo code for the simulations are found in Appendix B.1.

For the recruitment phase we can describe the process similar to transition probability in Eq. 2.2. First the description the probability distributions used in progeny production,

$$\text{Poisson} \left( R_i = \text{Gamma} \left( k_D, \frac{\text{Gamma}(k_E, \frac{R}{k_E})}{k_D} \right) \right). \quad (2.7)$$

Then following with the density dependent survival through random number generation:

$$r \sim U[0,1] < e^{-\alpha n} \tag{2.8}$$

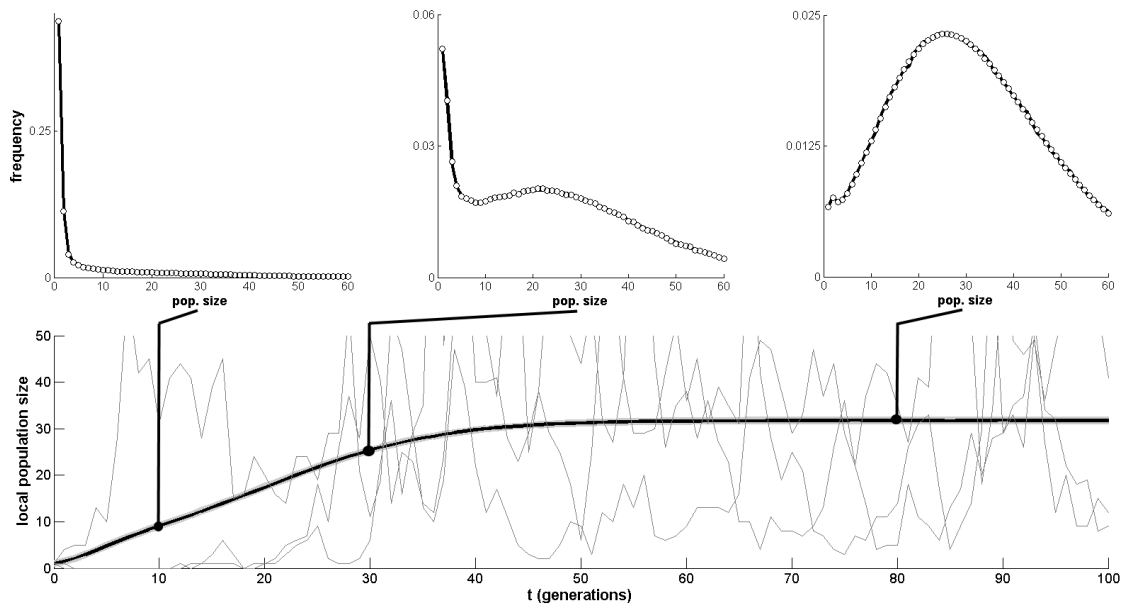
In Eq. (2.8)  $r$  is uniformly distributed random variable, which, if smaller than the survival probability, indicates that a specific individual survives to adulthood.

During the dispersal phase we adapt Eq. (2.4) to determine which individuals emigrate. An individual emigrates if

$$r \sim U[0,1] < m, \tag{2.9}$$

where  $r$  is again a uniformly distributed random variable. A migrant can then select any of the  $N$  patches uniformly random to immigrate into.

Comparing the full stochastic simulation to the deterministic approximation, Fig. 2.2, as expected we see the numerical simulations matching the analytical equations. While individual patch populations sizes fluctuate randomly around the mean, the mean of all patch populations is identical to the deterministic approximation. In the quasi steady-state the frequency distribution of population sizes is almost Gaussian as concluded by [17]. Further analysis of the transition probabilities is performed in Appendix B.2



**Figure 2.2.:** The smooth time (generations) evolution of a metapopulation simulation for the local environmental model. A quasi-steady state is achieved and frequency distribution in the top figures shows the presence of a Gaussian-like distribution in the steady state. Individual populations are constantly fluctuation (thin gray lines) while the mean of stochastic simulation (white dots in top graphs) compares well with the deterministic case (solid, thick line). Similar to Fig. 1 in [23]. Parameters  $R = 1.5$ ,  $\alpha = 0.01$ ,  $m = 0.02$ ,  $k_D = 1$ ,  $k_E = 10$  and stochastic simulations have  $N = 10000$  patches



# 3. Global Environmental Stochasticity

Through stochastic simulations we can compare the local environmental fluctuations to global fluctuations. We vary only the parameter determining the strength of the environmental stochasticity  $k_E$ . To provide for a specific and clear comparison the recruitment rate  $R$ , density dependent survival  $\alpha$ , migration rate  $m$  and demographic stochasticity strength  $k_D$  is kept constant .

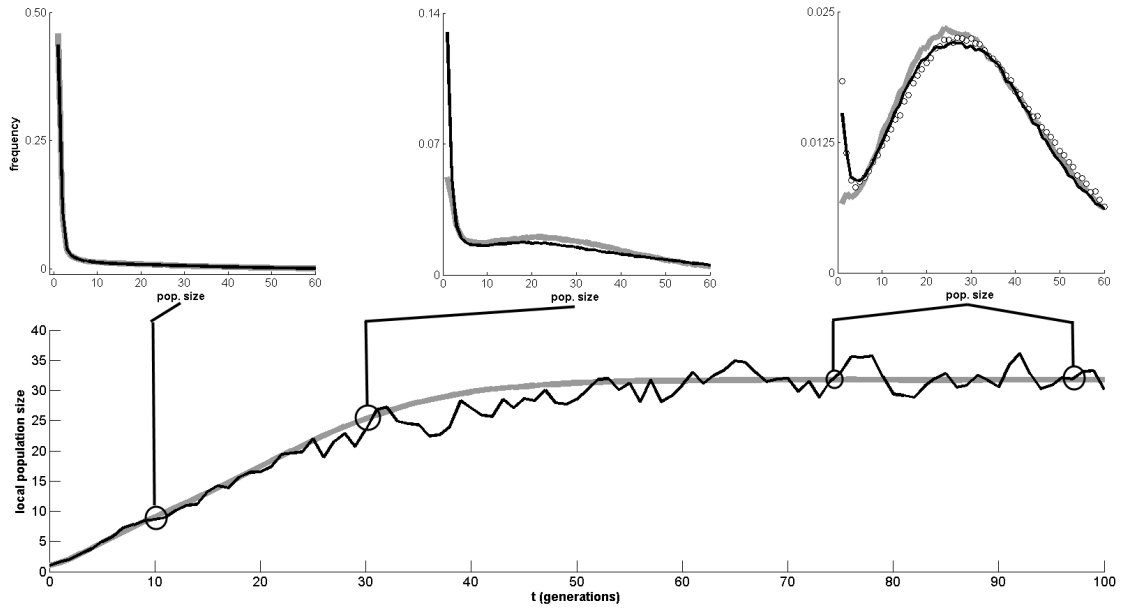
## 3.1. Weak Environmental Stochasticity

To create an initial feeling for global environmental stochasticity we present a simulation with weak environmental fluctuations, Fig. 3.1. Starting from an initial population size of unity for all patches, we found the mean population size evolves similarly for both global and local fluctuations. The trend for global stochasticity does not evolve smoothly and although it achieves a quasi steady-state it continuously fluctuates with no clear mean. This is already an indication that global fluctuations affects populations more intensely.

Using frequency distributions of patch population sizes we can compare the evolution of the population over generations. The distributions for global vs the local environmental model is quite similar, the only large deviations found are unoccupied and small population sizes. In the case of global environmental fluctuations there is more patches with a low number of inhabitants. This trend continues throughout, compare Fig. 3.2, and will form a central part of our analysis.

To support that there is no clear mean population size for global environmental model, we look at two different generations, generation 75 and 98. The mean local population size is almost exactly the same, but in Fig. 3.1 top right the frequency distributions still differ (dots versus black line). For local environmental stochasticity the frequency distributions compared between different generations will be identical in the steady-state, this is not the case for global environmental stochasticity.

For weak environmental stochasticity the proportion of occupied patches is almost the same in the quasi steady-state, Fig. 3.2. In the case of global environmental fluctuations the metapopulation takes longer to achieve the quasi steady-state. A metapopulation enduring global fluctuations will thus recover more slowly from a disaster, leaving these metapopulations more at risk to extinction.

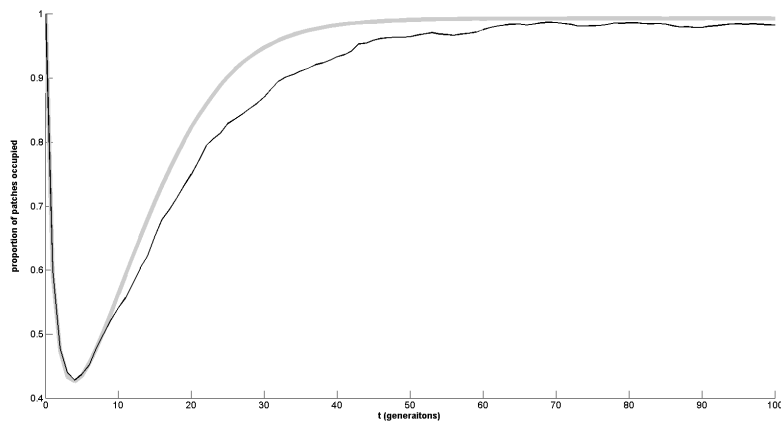


**Figure 3.1.:** The evolution of metapopulation dynamics over time for local (thick gray line) and global environmental stochasticity (thin black line). The metapopulation subject to global fluctuations follows the same evolution trend although no clear mean is achieved. The frequency distributions of population sizes are also similar, although there is always more patches in an unoccupied state for the case of global fluctuations. Top right figure includes a second frequency distribution (circles) of global environmental fluctuations from a comparable, yet different, generation. Parameters  $R = 1.5$ ,  $\alpha = 0.01$ ,  $m = 0.02$ ,  $k_D = 1$ ,  $k_E = 10$  and stochastic simulations have  $N = 10000$  patches with metapopulations realizations averaged 50 times.

## 3.2. Strong Environmental Stochasticity

For strong environmental fluctuations the effects of global stochasticity can be even more severe. In Fig. 3.3 we can see the metapopulation subjected to global environmental stochasticity stabilizes in a region of lower average local population size. Again we witness that the fraction of occupied patches is lower.

The high number of unoccupied patches can be the reason behind the substantially lower average population size. Fig. 3.4 depicts exactly the difference in the occupation proportion. It will be important to see how the rescue effect will work in a metapopulation where the occupation rate is a critical factor and if indeed the difference is substantial.

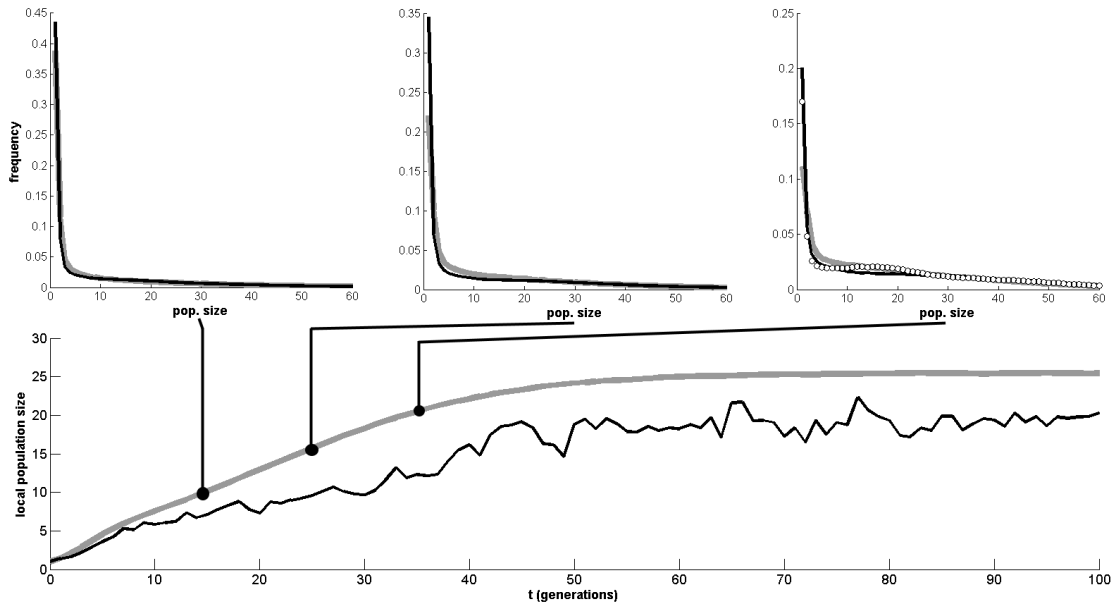


**Figure 3.2.:** The evolution of the proportion of patches in the metapopulation that is occupied. The local environmental stochastic metapopulation (thick gray line) recovers more quickly from an initial per patch population of unity than the metapopulation enduring global environmental stochasticity (black line). Parameters  $R = 1.5$ ,  $\alpha = 0.01$ ,  $m = 0.02$ ,  $k_D = 1$ ,  $k_E = 10$  and stochastic simulations have  $N = 10000$  patches with metapopulations realizations averaged 50 times.

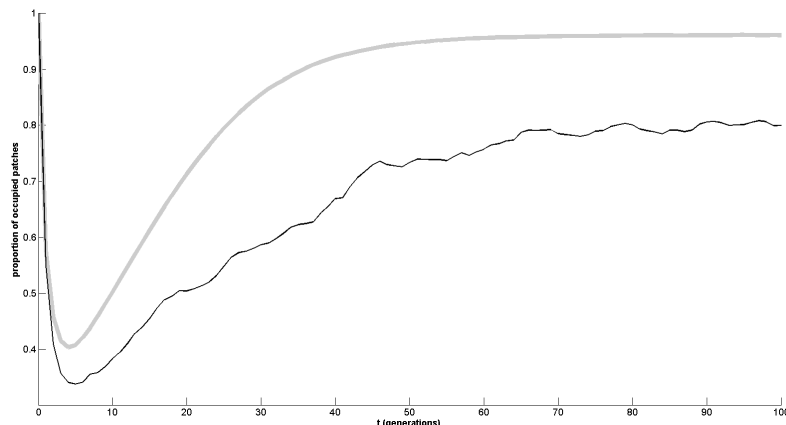
### 3.3. Observing Patch Populations

One important realization is how individual patch population react differently under global environmental stochasticity. In Fig. 3.5 we present two instances of patch populations for the local environmental model. The size of the patch populations fluctuate wildly as it is subjected to the whims of stochasticity. Once the metapopulation is in the quasi steady-state there is relatively little chance of a patch going extinct and if it does, it is quickly recolonized.

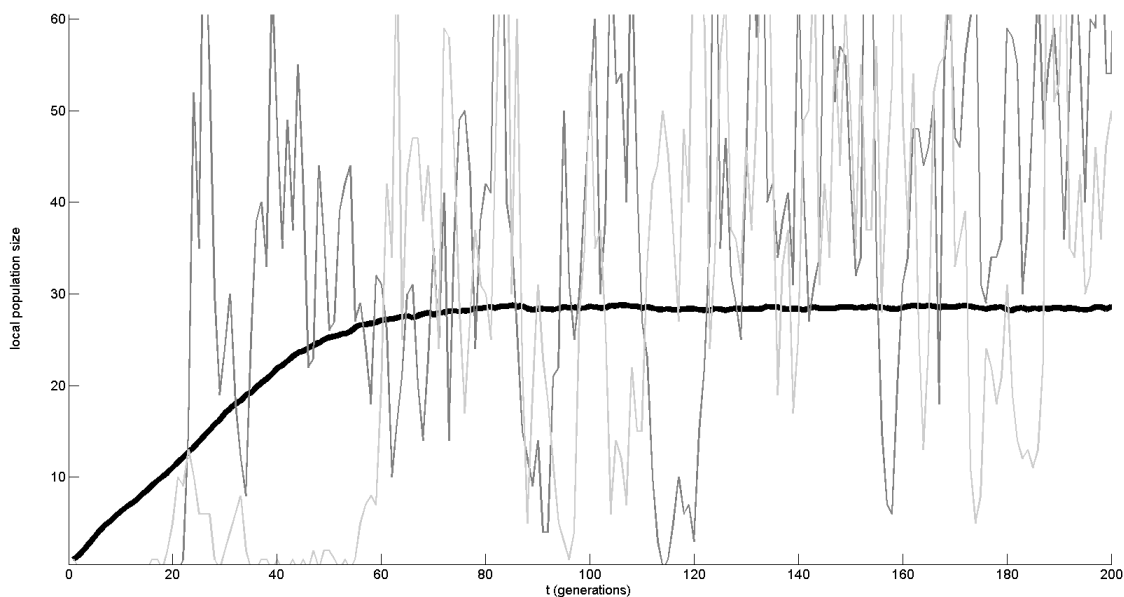
The same cannot be applied to a metapopulation subject to global environmental stochasticity. While the mean size of all patches fluctuates wildly, we can see the reason why. Global fluctuations affect all patch populations equally and simultaneously. This causes a correlation between patch size fluctuations. In Fig. 3.6 the patch sizes become more aligned once the simulation has achieved the quasi steady-state. We can interpret that if a metapopulation is currently enduring an adverse environment, a single patch that went extinct will have little chance of being recolonized by other patches in the population. All patches are enduring the stressful environment, and need to recover before they can send migrants to unoccupied patches.



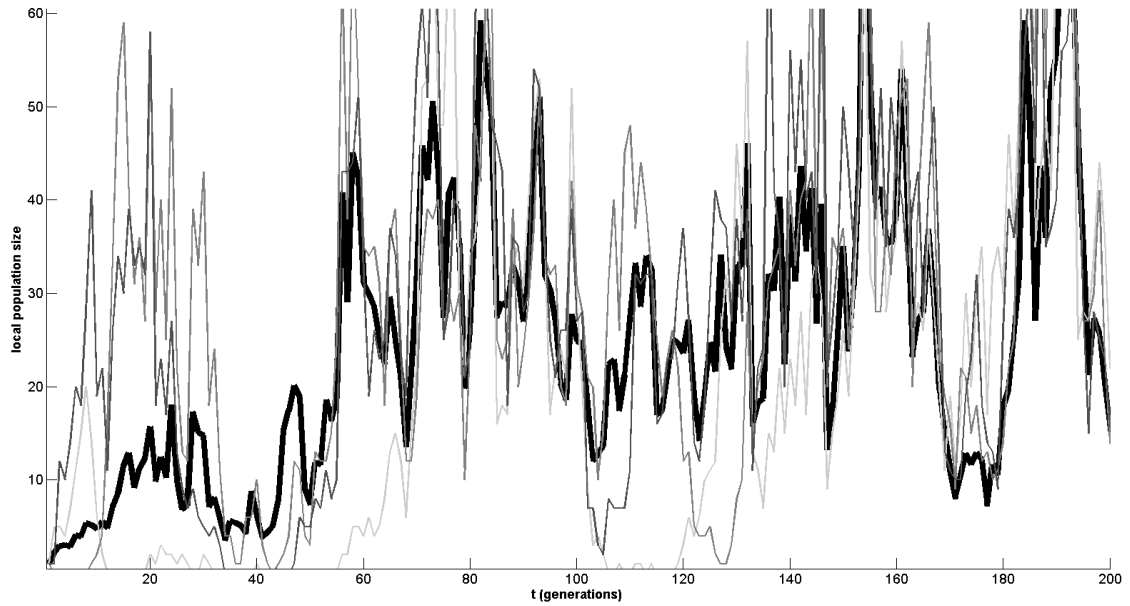
**Figure 3.3.:** For strong environmental stochasticity we observe the evolution of a metapopulation over time starting from all initial patch populations of unity. The metapopulation experiencing local environmental stochasticity still evolves smoothly over time into a quasi steady-state, whereas the metapopulation experiencing global fluctuations does not achieve a steady-state in the same region as that of local environmental model. We can see metapopulations experiencing global fluctuations are much more sensitive to the strength of environmental stochasticity. Parameters  $R = 1.5$ ,  $\alpha = 0.01$ ,  $m = 0.02$ ,  $k_D = 1$ ,  $k_E = 5$  and stochastic simulations have  $N = 10000$  patches with metapopulations realizations averaged 50 times. Frequency plots, top, conditioned on having the same instantaneous mean population size.



**Figure 3.4.:** The proportion of occupied patches as the simulation evolves over time. We can see the metapopulation experiencing global environmental stochasticity (black line) stabilizing at a lower proportion of occupation than a metapopulation experiencing local fluctuations (thick gray line). Parameters  $R = 1.5$ ,  $\alpha = 0.01$ ,  $m = 0.02$ ,  $k_D = 1$ ,  $k_E = 5$  and stochastic simulations have  $N = 10000$  patches with metapopulations realizations averaged 50 times.



**Figure 3.5.:** Patch populations (2 instances of patches shown) subjected to local environmental stochasticity (thin gray lines) fluctuate seemingly random about the mean of the entire metapopulation (thick black line). Parameters  $R = 1.5$ ,  $\alpha = 0.01$ ,  $m = 0.02$ ,  $k_D = 1$ ,  $k_E = 5$  and stochastic simulations have  $N = 10000$  patches with only one metapopulation realization.



**Figure 3.6.:** The individual patch population (3 shown, thin gray lines) in a metapopulation experiencing global environmental stochasticity follows the trend of the mean for the metapopulation (thick black line). Due to global fluctuations affecting all patches equally, it produces an effect of correlation between patch sizes. Parameters  $R = 1.5$ ,  $\alpha = 0.01$ ,  $m = 0.02$ ,  $k_D = 1$ ,  $k_E = 5$  and stochastic simulations have  $N = 10000$  patches with only one metapopulation realization.

## 4. The Rescue Effect

In section 1.1 we defined the rescue effect as saving a patch from extinction when it is on the brink of extinction. Following the process presented in [23] we can measure the strength of the rescue effect through analyzing the rate of local extinction. This proves to be more challenging than anticipated and will require careful explanation.

### 4.1. Measuring the Strength of the Rescue Effect

To measure the strength of the rescue effect we look at rate of local extinction. This is the rate at which patches that were previously occupied produces no progeny and thus go extinct due to local dynamics. A lower rate of local extinction, among other factors, could imply a higher strength of the rescue effect. Patches on the brink of extinction is saved from extinction by an immigrant, thus preventing the possibility of going extinct. The rate of local extinction evolves from the initial state of the population until it reaches a steady state, Fig. 4.1. For global environmental stochasticity we expected to see a much higher rate of local extinction. It is indeed not the case, the rates are almost similar for global and local fluctuations.

In our simulation the process of calculating the number of offspring an adult produces follows exactly the same process for local and global environmental models. This can imply that the rate can be the almost the same in both models. Remember, the rate of local extinction is measured as the number of patches that produced zero progeny in this generation divided by the number of patches that is capable (occupied) of producing progeny at the beginning of the generation. The more apparent difference in proportion of occupied patches, as seen in Fig. 4.1 is then due to patches being recolonized at a slower rate for global environmental fluctuations.

Although the measurement provided us with some valuable insight into the capabilities of global environmental stochasticity, it does not clearly describe the rescue effect as in the case for local environmental stochasticity. The largest concern is if the local rates of extinction is almost similar, why are patches recolonized at a slower rate, resulting in a lower proportion of occupied patches and subsequently a lower mean population size.

## 4.2. Measuring the Occupancy Rate

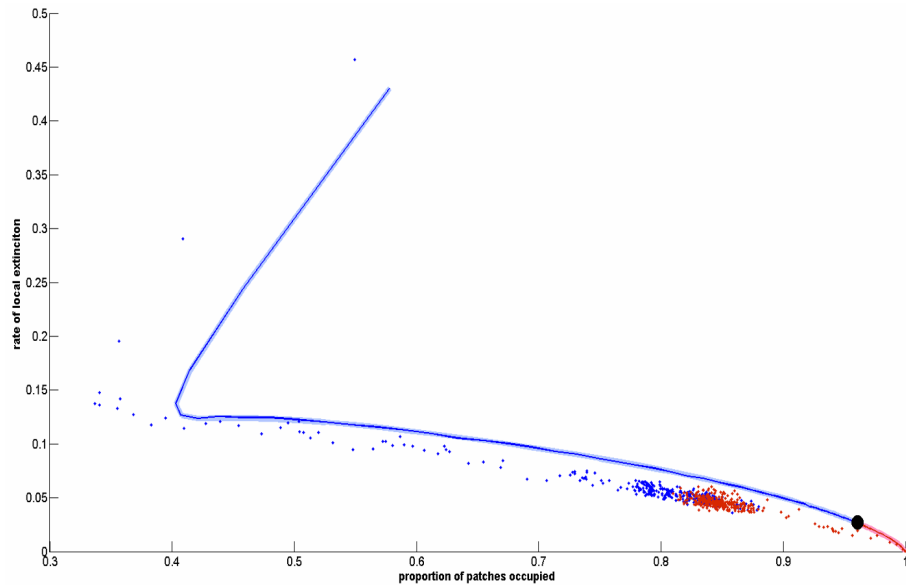
Taking a look at the lower occupancy rate for global environmental stochasticity, we decided to determine at what rate a population patch receives immigrants, possibly rescuing it from extinction. In a simulation we count the number of times a patch receives an immigrant in a generation and record the current size of the patch. The size of the patch is recorded after dispersers have left their native patches, but before immigration happens, see section (2.1.2). From these measurements we produce the result in Fig. 4.2 by dividing for the total number of occurrences of a patch size in the complete simulation. It is immediately clear the rate at which patches in a metapopulation subjected to local stochasticity receives immigrants is constant, regardless of patch population size. This phenomenon can be inferred from the uncorrelated patch sizes in the local environmental model, see Fig. 3.5.

A higher number of immigrants per patch size indicates a stronger rescue effect. At low population sizes we see a weaker rescue effect in the global environmental model. For accurate comparison we also show what the rate of receiving immigrants would be like if, in the local model, the patch occupancy rate was the same as for the global. This indicates that only at population sizes below sixteen do we see a weaker rescue effect in the global model.

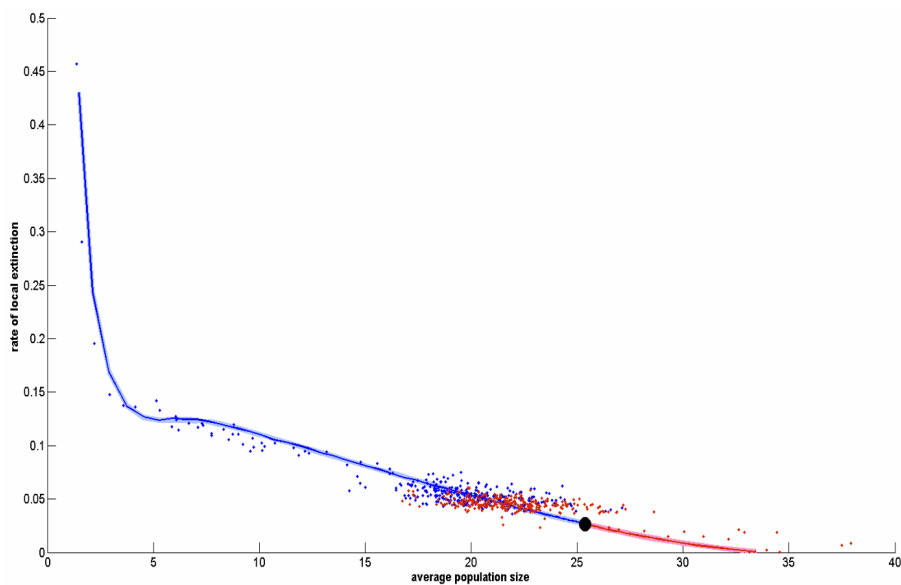
Comparing global environmental stochasticity we see that the rate at which patches receives immigrants increases with patch size. The first element contributing to this effect is that patch sizes are correlated, see Fig. 3.6. All patches simultaneously experience favorable environmental effects, resulting in a large number of migrants. To clarify the sudden lower than expected rate of receiving immigrants for extinct populations patches, we take a closer look at the dynamics. A patch must be recolonized before it can start producing progeny, but due to all patches being in a bad state, recolonization does not happen immediately. The extinct patch has to wait until the other patches, that survived unfavorable environmental circumstances, are large enough to produce migrants. A patch that is extinct will compete with all the other patches that are currently also extinct for migrants. These combined effect produce a much lower rate of receiving immigrants than expected.

Further, the interesting observation is the sudden rise in the rate of populations patches of small size. It is an effect of patches coming out of extinction by receiving an immigrant (or maybe 2), recolonizing the patch. Overall it shows why the presence of at least one offspring producing individual is critical for the metapopulation as a whole, but also a metapopulation experiencing unfavorable environmental effects will, most likely, not be able to rescue itself.



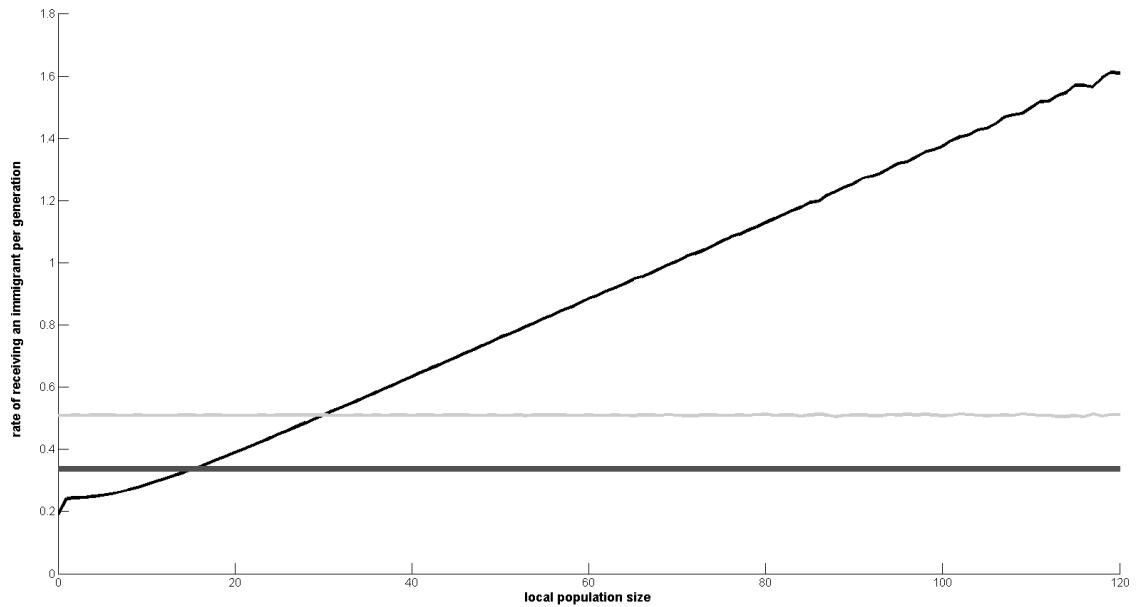


(a)



(b)

**Figure 4.1.:** Examining the strength of the rescue effect. We start the simulations above (red lines) and below (blue lines) the steady state (black dot). It quickly, within 5 generations, relaxes to the slow trajectory [23] and continues until it reaches the steady state. The thick lines represent the deterministic limit, the solid line the stochastic simulation for local environmental stochasticity and the dotted trends are for global environmental model. Both (a) and (b) have the same values on the y-axis, the x-axes present the two important measurements defining the current state of the population, namely, proportion of occupied patches and average patch population size. Parameters  $R = 1.5$ ,  $\alpha = 0.01$ ,  $m = 0.02$ ,  $k_D = 1$ ,  $k_E = 5$  and stochastic simulations have  $N = 10000$  patches averaged over 50 metapopulation realizations.



**Figure 4.2.:** The rate at which a population patch receives an immigrant in a generation compared to its size. The size of a patch is measured after dispersers have left the patch, but before migrants arrive. The black trajectory is for global fluctuations, showing a positive correlation between number of immigrants and patch size, while the thin gray line is for local fluctuations at the same parameter settings. Lastly the thick gray line is adjusted for the local environmental population to have the same rate of occupancy in the steady state. Parameters  $R = 1.5$ ,  $\alpha = 0.01$ ,  $m = 0.02$ ,  $k_D = 1$ ,  $k_E = 5$  and stochastic simulations have  $N = 10000$  patches averaged over 50 metapopulation realizations.

## 5. Conclusion

The discrete stochastic Ricker model offers a very robust platform for simulating metapopulations. Parameters can be varied for a wide range of possible application producing clear results. In the case of a low number of patches,  $N$  small, the dynamics are not robust, and other models could be used [23]. The discrete time generations also require a large number of generations. Empirically, species with a long life cycle will be difficult to evaluate. For local environmental stochasticity the model has been empirically tested by [21], providing for the eligibility of the model. The next step would be to verify the effects witnessed in the global environmental model in an empirical environment. This is notably more difficult as all patches need to be influenced simultaneously and equally. We suggest the resulting simulated effects of a metapopulation enduring global environmental stochasticity requires necessarily for such a study. The much higher extinction risk of such a fragmented population can then be further assessed. It could also give an indication for the validity of using a Gamma distribution to induce global environmental stochasticity through modification of the birth rate. The Gamma distribution could be too harsh a measure for modifying the birth rate and an alternative distribution which is less severe on the birth rate could be presented.

The correlated size of patch populations in the global model causes a metapopulation to have difficulty rescuing itself from extinction. It is an important observation as the risk of extinction for the metapopulation is especially sensitive to the reproduction rate. We used a reproduction rate throughout of  $R = 1.5$ , as lower rates produce a very sensitive population. We showed that a metapopulation with a large number of patches is capable of recovering from a perturbation of reducing all patches to population size unity, for both the local and global model. The metapopulations achieve a quasi steady-state where it will continue until a series of chance stochastic events must eliminate the population. A metapopulation with global environmental stochasticity still achieves a steady state, although it is constantly fluctuation in this steady state region and there is no clear mean for the population. The strength of environmental stochasticity is important, as metapopulations enduring global fluctuations experience the fluctuations much stronger. As the strength of the stochasticity is increased the difference in average population size and proportion of occupied patches for global compared to local fluctuations becomes more pronounced .

Surprisingly the rate of local extinction and patch occupancy rate is not substantially different in the case of global environmental stochasticity, deviating only slightly.

The strength of the rescue effect is seemingly similar in the two models. An important question to answer is, what causes the similarity and if the rescue effect is still active the global environmental model? We measured the rate at which a patch receives an immigrant in a generation based on its population size, and found that in the case of local environmental fluctuations the rate is constant. This is in accordance with the effect of uncorrelated patch sizes in the steady-state. On the other hand, metapopulations with global environmental stochasticity have an increasing rate of receiving migrants for increasing patch population size. The rescue effect is still present in these populations, but it is easily overshadowed by stronger stochasticity that could drive patches to extinction. For small population sizes the rescue effect is also found to be weaker in the global environmental model.

Further evaluation will look at the path to extinction. Eriksson *et al.* [16] computed the path for the local environmental model (figure 10) and found populations typically approached extinction gradually. Does a metapopulation experiencing global fluctuations go extinct due to a sudden very low birth rate or successive adverse environmental effects? The existence of the rescue effect can be verified if it is found the metapopulation does not succumb when experiencing a sudden, low birth rate.

Global environmental stochasticity is a critical factor for populations studies. To recognize the effects of global environmental stochasticity in empirical metapopulation, one can look at the correlation of population sizes. In such a case the necessary precautions can then be implemented in a timely fashion to prevent global extinction.

# Bibliography

- [1] Richard Levins. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the ESA*, 15(3):237–240, 1969.
- [2] Ilkka Hanski. *Metapopulation Ecology*. Metapopulation Ecology. OUP Oxford, 1999.
- [3] Nicholas J. Gotelli and Walter G. Kelley. A general model of metapopulation dynamics. *Oikos*, 68(1):pp. 36–44, 1993.
- [4] Ilkka Hanski. Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of the Linnean Society*, 42(1-2):17–38, 1991.
- [5] Ilkka Hanski and Michael Gilpin. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society*, 42(1-2):3–16, 1991.
- [6] Jana Verboom, Alex Schotman, Paul Opdam, and Johan A. J. Metz. European nuthatch metapopulations in a fragmented agricultural landscape. *Oikos*, 61(2):pp. 149–156, 1991.
- [7] PER Sjögren. Extinction and isolation gradients in metapopulations: the case of the pool frog (*rana lessonae*). *Biological Journal of the Linnean Society*, 42(1-2):135–147, 1991.
- [8] Alan Hastings and Carole L. Wolin. Within-patch dynamics in a metapopulation. *Ecology*, 70(5):pp. 1261–1266, 1989.
- [9] J.A.J. Metz and O. Diekmann. *The Dynamics of Physiologically Structured Populations*. Lecture Notes in Biomathematics. Springer-Verlag, 1986.
- [10] James H. Brown and Astrid Kodric-Brown. Turnover rates in insular biogeography: Effect of immigration on extinction. *Ecology*, 58(2):445–449, March 1977.
- [11] Ilkka Hanski. Dynamics of regional distribution: The core and satellite species hypothesis. *Oikos*, 38(2):pp. 210–221, 1982.
- [12] Alan Hastings. Structured models of metapopulation dynamics. *Biological Journal of the Linnean Society*, 42(1-2):57–71, 1991.
- [13] Russell Lande, Steinar Engen, and Bernt-Erik Sæthøer. Extinction times in finite metapopulation models with stochastic local dynamics. *Oikos*, 83(2):pp. 383–389, 1998.

- [14] Martin Drechsler and Christian Wissel. Separability of local and regional dynamics in metapopulations. *Theoretical Population Biology*, 51(1):9 – 21, 1997.
- [15] T.J. Newman, Jean-Baptiste Ferdy, and C. Quince. Extinction times and moment closure in the stochastic logistic process. *Theoretical Population Biology*, 65(2):115 – 126, 2004.
- [16] A. Eriksson, F. Elías-Wolff, and B. Mehlig. Metapopulation dynamics on the brink of extinction. *Theoretical Population Biology*, 83(0):101 – 122, 2013.
- [17] Kevin Higgins. Metapopulation extinction risk: Dispersal’s duplicity. *Theoretical Population Biology*, 76(2):146 – 155, 2009.
- [18] Willy Feller. Die Grundlagen der Volterraschen Theorie des Kampfes ums Dasein in wahrscheinlichkeitstheoretischer Behandlung. *Acta Biotheoretica*, 5(1):11–40, 1939.
- [19] Jonathan Roughgarden. A simple model for population dynamics in stochastic environments. *The American Naturalist*, 109(970):pp. 713–736, 1975.
- [20] R.M.C. May. *Stability and Complexity in Model Ecosystems*. Landmarks in Biology Series. Princeton University Press, 2001.
- [21] Brett A. Melbourne and Alan Hastings. Extinction risk depends strongly on factors contributing to stochasticity. *Nature*, 454(7200):100–103, July 2008.
- [22] Bruce E. Kendall and Gordon A. Fox. Unstructured individual variation and demographic stochasticity. *Conservation Biology*, 17(4):1170–1172, 2003.
- [23] Anders Eriksson, Federico Elías-Wolff, Bernhard Mehlig, and Andrea Manica. The emergence of the rescue effect from explicit within- and between-patch dynamics in a metapopulation. *Proceedings of the Royal Society B: Biological Sciences*, 281(1780), 2014.
- [24] W. E. Ricker. Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, 11(5):559–623, 1954.
- [25] N.L. Johnson, A.W. Kemp, and S. Kotz. *Univariate Discrete Distributions*. Wiley Series in Probability and Statistics. Wiley, 2005.
- [26] N.L. Johnson, S. Kotz, and N. Balakrishnan. *Continuous univariate distributions*. Number v. 2 in Wiley series in probability and mathematical statistics: Applied probability and statistics. Wiley & Sons, 1995.
- [27] Peter L. Chesson. Models for spatially distributed populations: The effect of within-patch variability. *Theoretical Population Biology*, 19(3):288 – 325, 1981.
- [28] Robert M. May. Stability in randomly fluctuating versus deterministic environments. *The American Naturalist*, 107(957):pp. 621–650, 1973.

# A. Alternative Continuous Time Model

## A.1. Continuous time Metapopulation Model

For comparison to the discrete generation metapopulation model we study, I briefly present the alternative, although similar, dynamics of stochastic, individual-based continuous time metapopulation models as found in [16].

A metapopulation consists of  $N$  connected patches, where each patch has its own independent birth-death dynamics. The within patch birth and death rates for a specific time  $t$  are expressed as

$$b_i(t) = ri, \tag{A.1}$$

$$d_i(t) = \mu i + (r - \mu)i^2/K, \tag{A.2}$$

where  $i$  is the patch population size,  $r$  is the per-capita birth rate and  $\mu$  the per-capita mortality rate. The sources of stochasticity can be included in the form of noise, directly modifying the birth and death rates. It is not included here. The independent per patch migration rate  $m$  is dependent on the size of the patch:

$$m_i = mi. \tag{A.3}$$

After emigrating, dispersers join a common pool of  $M$  migrants. Immigration of migrants into a patch from the pool happens with rate

$$I = \frac{\eta M}{N}. \tag{A.4}$$

The rate of mortality during migration is  $\eta$ .

To consider numerical simulations the population evolves in time steps according to the summation of the rates, Eqs. (A.1)-(A.4), to the next event  $\Lambda_k$ , for patch  $k$ . If patch  $k$  contains  $i$  individuals we have the sum:

$$\Lambda_k = b_i + d_i + m_i. \quad (\text{A.5})$$

To account for the whole metapopulation, events will happen with rate  $\Lambda = \sum_k \Lambda_k$ ,  $k = 1, \dots, N$ . The continuous time model for metapopulations thus proceeds through exponentially distributed random events with an expected value  $1/\Lambda$ . Lastly, a master equation can be produced for the contribution to  $d\rho/dt$  from all events.  $\rho$  is the probability of a patch having  $i$  individuals. Considering all possible transitions which modify the populations size by +1 or -1 and writing the equation in terms of raising and lowering operators  $\mathbb{E}_j^\pm$  the change in probability over time will be:

$$\begin{aligned} \frac{d\rho}{dt} = & \sum_{j=0}^{\infty} \left( \mathbb{E}_j^+ \mathbb{E}_{j+1}^- - 1 \right) b_j n_j \rho + \sum_{j=0}^{\infty} \left( \mathbb{E}_j^+ \mathbb{E}_{j+1}^- - 1 \right) d_j n_j \rho \\ & + \frac{1}{N} \sum_{i=1}^{\infty} \sum_{j=0}^{\infty} \mathbb{E}_{i-1}^- \mathbb{E}_i^+ \mathbb{E}_j^+ \mathbb{E}_{j+1}^- m_i n_i (n_j - \delta_{ij} + \delta_{i-1j}) \rho - \sum_{i=1}^{\infty} m_i n_i \rho \quad (\text{A.6}) \end{aligned}$$

Here  $n_j$  is the number of patches containing  $j$  individuals. Assuming instantaneous migration:  $\eta \rightarrow \infty$  and  $\mu = 1$ .



## B. Numerical Simulations

### B.1. Pseudo Code for Discrete Time Stochastic Simulations

Local environmental stochasticity affects each patch separately. For a full stochastic simulation the pseudo code is quite simple, here is a skeleton for the sequential code. The local dynamics are contained in the iterations over all patches, contrary to the case of global environmental stochasticity following below.

---

```
initialize adults_in_patch
N = total number of patches
R = recruitment rate
kE = shape parameter environmental stochasticity
kD = shape parameter demographic stochasticity
alpha = density dependent survival
m = rate of dispersal

loop over generations
  for all patches
    MeanRE = Gamma(kE,R/kE)
    for each individual in patch
      Ri = Gamma(kD,meanRE/kD)
      offspring = Poisson(Ri)

      for each offspring
        r = U[0,1]
        if r<exp(-alpha*adults_in_patch)
          offspring_survives =+ 1
        end
      end
      children_in_patch =+ offspring_survives
    end
  end
end

for each patch
```

```

    for each children_in_patch
      r = U[0,1]
      if r < m
        M =+ 1
        children_in_patch =- 1
      end
    end
  end

  for each M
    r = U[1,N]
    children_in_patch(r) =+ 1
  end

  for each patch
    adults_in_patch = children_in_patch
  end
end

```

---

For global environmental stochasticity the code is similar, as discussed in section 1.2.1 the global fluctuations affect all patch populations equally. The difference in code is the rate modified before calculating the local stochasticity.

---

```

initialize adults_in_patch
N = total number of patches
R = recruitment rate
kE = shape parameter environmental stochasticity
kD = shape parameter demographic stochasticity

loop over generations
  MeanRE = Gamma(kE,R/kE)
  for all patches
    for each individual in patch
      Ri = Gamma(kD,meanRE/kD)
      offspring = Poisson(Ri)

      for each offspring
        r = U[0,1]
        if r < exp(-alpha*adults_in_patch)
          offspring_survives =+ 1
        end
      end
    end
  end
end

```

```

        children_in_patch ==+ offspring_survives
    end
end

for each patch
    for each children_in_patch
        r = U[0,1]
        if r < m
            M ==+ 1
            children_in_patch ==- 1
        end
    end
end

for each M
    r = U[1,N]
    children_in_patch(r) ==+ 1
end

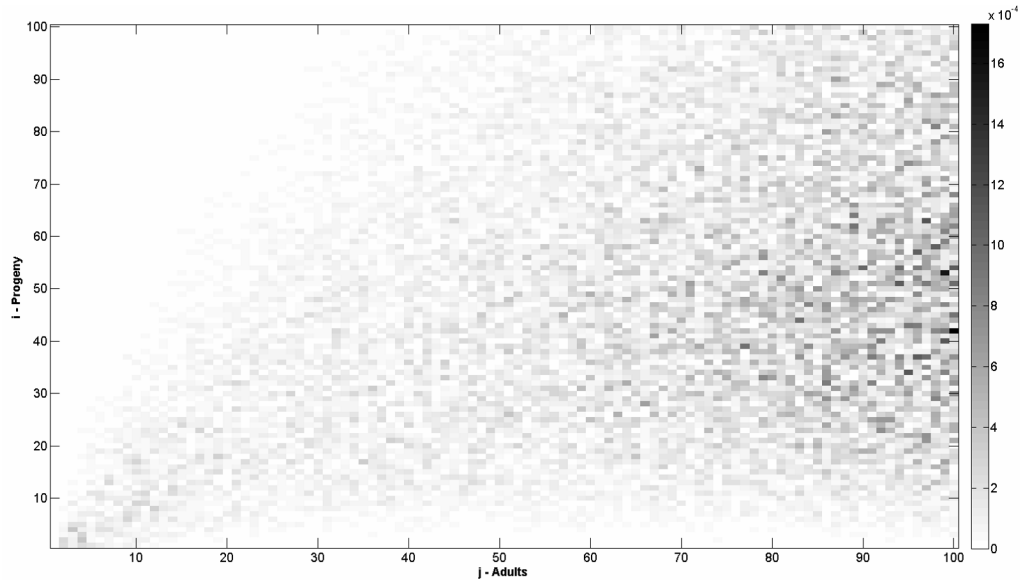
for each patch
    adults_in_patch = children_in_patch
end
end

```

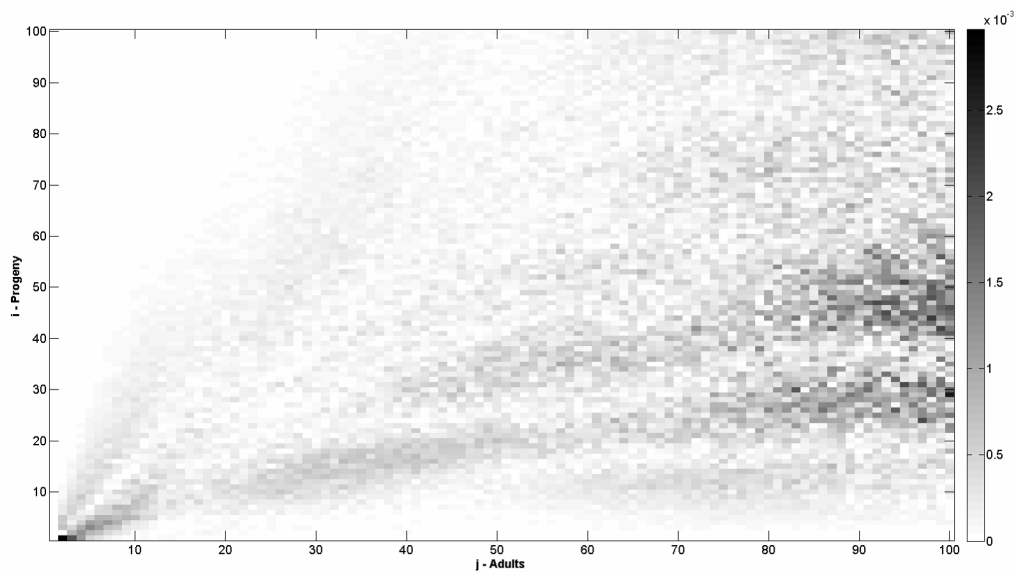
---

## B.2. Transition Probabilities

For the deterministic limit we use the analytical eq. 2.2 to explicitly calculate matrix. Using our numerical simulations we can compute these transition probabilities by counting the number of times a population with  $j$  adults results in  $i$  progeny. Averaging enough times over these simulations should agree with the analytical equation, that is, in the local environmental stochastic model. In *fig. Fig. B.1(a)* we see the results. While the simulation does not agree exactly, the absolute deviation in values is very small, especially around the origin where the dynamics is critical. For global fluctuations we find that the deviation is an order of magnitude higher, although still small. Noticeably we find that the deviation is large around the origin, depicting the slightly higher probability for a patch to go extinct if at small population size, it also shows that such a patch has little chance of being rescued. The rescue effect rather acts on patches further away from extinction (population size of zero).



(a)



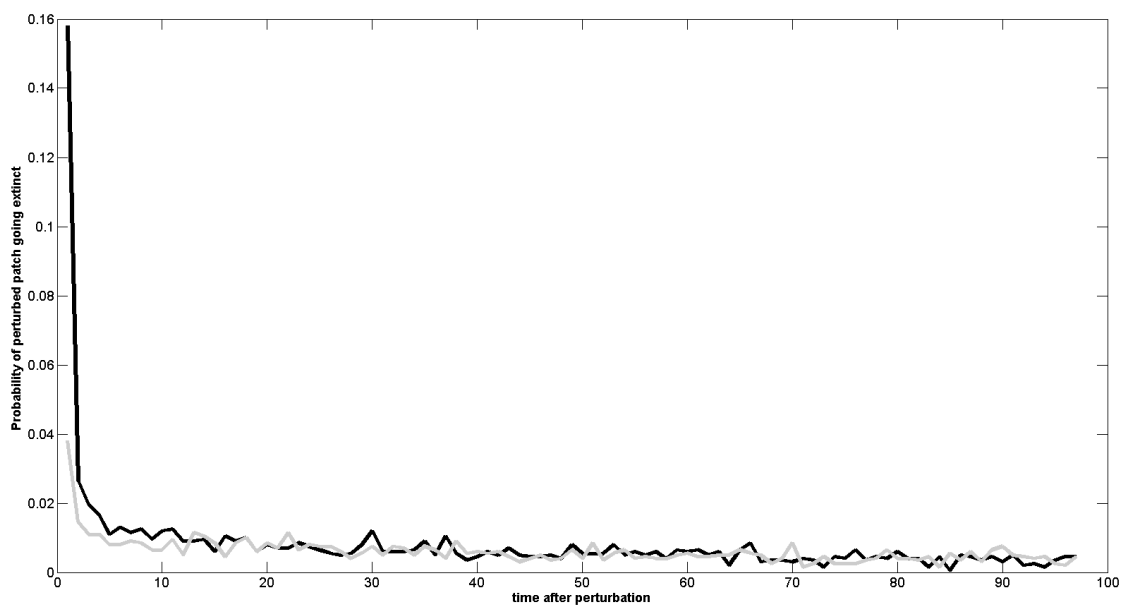
(b)

**Figure B.1.:** Measuring the deviation of transition probabilities for  $j$  adults producing  $i$  progeny. (a) compares the local environmental stochastic simulations to the analytical framework and the deviation is found to be in the order of  $10^{-4}$ . (b) compares global environmental stochastic simulations with the analytical framework, the deviation is much larger, in the order of  $10^{-3}$ . Parameters  $R = 1.5$ ,  $\alpha = 0.01$ ,  $m = 0.02$ ,  $k_D = 1$ ,  $k_E = 5$  and stochastic simulations have  $N = 10000$  patches averaged over 50 metapopulation realizations

# C. Patch Perturbations

## C.1. Perturbing a single patch

Most of the population simulations start from a perturbed state. We initialize all patches to either have a population size above or below the steady state. We also looked at single patch perturbations. To see how a patch recovers from a perturbation we first perturbed a single patch in the metapopulation to size unity and followed the recovery of the patch. This measure was too harsh, as a patch has very little chance to recover or be rescued before stochasticity drives it extinct. We thus rather, randomly, halved a single patch size and recorded the probability of a patch continuing its existence. In Fig. C.1 the patches enduring global fluctuations have, as expected, a higher probability of going extinct in the first generation after a perturbation. Surprisingly the probability becomes equal after the initial generations. The probability of the perturbed patch going extinct also slowly approaches zero, this is due to normal stochastic factors taking over and possibly driving the patch extinct even after it has recovered.



**Figure C.1.:** Perturbing a single patch in the population to half its size and following it until extinction. The thin gray line is for local fluctuations while the black line is for global fluctuations. Parameters  $R = 1.5$ ,  $\alpha = 0.01$ ,  $m = 0.02$ ,  $k_D = 1$ ,  $k_E = 5$  and stochastic simulations have  $N = 10000$  patches averaged over 50 metapopulation realizations